Conflict management in wild spider monkeys (*Ateles geoffroyi yucatanensis*)

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Abstract

Animals living in groups are frequently exposed to conflicts of interest which can escalate into aggression. Aggressive interactions may be a means to resolve incompatibility among objectives. Nevertheless, aggression may undermine the benefits of group living by disrupting the relationships between opponents. Thus, conflict management mechanisms have evolved to cope with the potential damage brought about by aggressive interactions. The aim of my thesis was to investigate the mechanisms to prevent aggressive escalation and to mitigate its negative consequences in 2 communities of wild spider monkeys (*Ateles geoffroyi yucanensis*). I also examined the factors, such as relationship characteristics, affecting the occurrence of these mechanisms. Spider monkeys live in communities with a high degree of fission fusion dynamics in which individuals frequently split and merge into subgroups of variable composition. The implications of this social system for conflict management were also explored.

To characterise spider monkeys' social relationships, two components were identified and labelled compatibility and risk. These components were further related to relationship characteristics, such as kinship, sex combinations, and tenure in the community. Kin had more compatible relationships than non kin, but there was no difference for risk. Male-male dyads were characterised as being significantly more compatible and riskier than either female-female dyads or male-female dyads. Furthermore, individuals with longer tenure had riskier relationships than individuals with shorter tenure.

Among the post-conflict management mechanisms spider monkeys did not engage in reconciliation, redirected aggression, or bystander affiliation. However, an option afforded by their high degree of fission fusion dynamics was used in the aftermath of aggression. Fission from former aggressors was more likely to occur within one hour of the aggressive conflicts than in control periods. Furthermore, individuals sharing riskier and less compatible relationships had significantly shorter latencies to fission compared to those with less risky and more compatible relationships. These patterns suggest that fission may function to reduce the possibility of renewed aggression and cope with increased post-conflict anxiety.

Indeed, anxiety levels were higher in the recipients of aggression during the first 5 post-conflict minutes compared to baseline levels.

Whereas fission may be a mechanism to cope with the negative consequences of aggressive escalation, fusion of subgroups could lead to uncertainty and hostility. Indeed, aggression increased in the first five post-fusion minutes compared to baseline levels. There was also an increase in post-fusion friendly behaviours, which may function as signals of good intentions. This view was confirmed as post-fusion aggression was reduced when friendly behaviours took place. In addition, shorter latencies of post-fusion aggression and friendly behaviours were found between individuals with riskier relationships compared to those with less risky relationships. Prevention of aggressive conflicts may also be achieved by adjusting subgroup size to the availability of feeding resources thereby reducing competition. The effectiveness of this flexible adjustment was demonstrated during a period of drastic reduction in food sources caused by two consecutive hurricanes at the field site. Mean subgroup size and fusion rates were significantly reduced in the post-hurricane compared to pre-hurricane periods.

Hence, my thesis adds to the study of social relationships and conflict management in non-human animals by making several contributions. I provided the first evidence of relationship components in new world monkeys. I then examined the potential of fission-fusion dynamics as a means to manage conflicts among community members. I was the first demonstrating that fission is a post-conflict mechanism. Fission from the former aggressor was especially used by individuals with riskier and less compatible relationships. Subgroup fusion increased aggressive conflicts, especially between individuals with riskier relationships, but post-fusion friendly behaviours reduced them. The effectiveness of fission-fusion dynamics in conflict management was further demonstrated by how the spider monkeys coped with the potential increase in conflict among community members due to a dramatic reduction in food supplies due to two hurricanes. Overall, spider monkeys appear to deal with conflicts using the full range of the flexible social options afforded by their social system.

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General Introduction

1.1 Living in groups

Cooperation is a powerful force shaping the social life of many different species, and for group-living species cooperation improves survival and reproduction in a given environment (van Schaik & Kappeler, 2006). Ecological factors, however, likely provide the ultimate selective pressures for animals to live in groups (Wrangham, 1987; Dunbar, 1988; Krebs & Davies, 1993). The primary selection pressures operating on animals have been summarised by Lee (1994) and are thought to include: predation, resource defence, foraging efficiency, access to mates, thermoregulation, cooperative care of young, enhanced information exchange and social learning. Each of these selective pressures conveys both benefits on individuals living in groups as well as costs. A further cost of group living includes disease transmission (Lee, 1994), which has no concomitant benefit.

1.1.1 Benefits of group living

Predation pressure is argued to play a major if not the key role among the selective forces responsible for the evolution of group living (van Schaik, 1983). Although observations of predation attacks are relatively rare (Anderson, 1986; Cheney & Wrangham, 1987), a growing body of observations of predation events demonstrates it is a phenomenon that impacts on a wide variety of primate species from the tiny callitrichids (marmosets and tamarins) to the great apes (Miller & Treves, 2007). Given that the ultimate consequence of a predator's attack on one individual could result in the total loss of future lifetime fitness benefits, even if the risk of being caught by a predator is low, strong selection pressure should operate in favour of behavioural mechanisms that prevent or reduce predation (Anderson, 1986). One way to reduce predation is through associating in multi-individual groups. Indeed, in gregarious species group size increases where predation risks are higher (Pulliman & Caracao, 1984). This is because the chances to be selected by a predator are reduced along with the increasing number

of potential prey. It is reasonable to argue that predation pressures may have forced most non-human primates in the direction of group life given that most of them are gregarious. Indeed, there are a variety of predators known to prey on monkeys species. Among the predators more commonly reported for African monkey species include leopards (*Panthera pardus*), lions (*P. leo*), large birds of prey (e.g., crowned eagle, *Stephanoaetus coronatus*), as well as chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*), whereas among new world monkeys key predators include jaguars (*P. onca*), pumas (*P. concolor*), ocelots (*Leopardus pardalis)*, harpy eagles (*Harpia harpyja*) and several species of snakes (Anderson, 1986; Condit & Smith, 1994).

With respect to predation, group living provides a number of benefits, including higher levels of vigilance given the number of "ears and eyes" involved in the detection of predators (Pulliman & Caracao, 1984; Stanford, 2002). van Schaik and colleagues showed that large groups of monkeys were more effective at detecting predators than small groups (van Schaik, van Noordwijk, Warsono & Sutriono, 1983). Conversely, capuchin (*Cebus olivaceus*) and vervet (*Cercopithecus aethiops*) monkeys in smaller groups spent more time scanning than those in large groups, demonstrating the direct risk associated with lower vigilance in small groups (capuchin monkeys, de Ruiter, 1986; vervet monkeys, Baldellou & Henzi, 1992; Treves, 1999). In gregarious species group size increases where predation risk is higher (Pulliman & Caracao, 1984). The detection of predators in primates of the Sumatran forest, proved to be more effective in large groups of monkeys rather than in small groups (van Schaik, 1983). Having sufficient group members to detect predators may mean that for some species polyspecific associations are needed to reap the full benefit of anti-predator detection when foraging and travelling. Several species of callitrichids are known to partner with another group of a different species and travel together throughout each day (red-bellied tamarins, *Saguinus labiatus* and saddle-back tamarins, *S. fuscicollis*, Buchanan-Smith, 1990; moustached tamarins, *S. mystax* and saddle-back tamarins, Smith, Kelez, &Buchanan-Smith, 2004). Furthermore, several species of guenons recognise the alarm calls of other species and benefit from associating in large polyspecific groups (Wolters & Zuberbuhler, 2003). Such polyspecific associations are not restricted to the primate taxa as, for

example, Thompson's (*Eudorcas thomsonii*) and Grant's gazelle (*Nanger granti*) also engage in polyspecific associations as an anti-predator strategy (Fitzgibbon, 1990).

Individuals further gain anti-predator benefits by living with other conspecifics because of increased predator defence. Individuals in the group can either passively defend or intervene actively in the defence of the preyed individual (Bartecki & Heyman, 1987). Alarm calls are one form of passive defence against predators by communicating a state of emergency to the other group member (Cheney & Seyfarth ,1981; Stanford, 2002). Furthermore, providing an alarm call can inform predators that they have been detected and therefore deter the efforts of ambush predators (Zuberbühler, 2000). More active defence against predators involves mobbing them or even attacking them. Mobbing appears to be a safer and more common strategy among smaller sized primates, but not the only one (Miller & Treves, 2007). For example, saddle-back tamarins successfully mob snakes (Bartecki & Heymann, 1987), and a moustached tamarin was rescued by other group members after being caught by a boa, involving direct confrontation with the snake (Tello, Huck & Heymann, 2002). Furthermore, a group of white-faced capuchin monkeys (*C. capuchinus*) responded to an attack of boa constrictor by several adult members of the group repeatedly throwing sticks at the snake and harrassing it (Chapman, 1986).

Although the selective pressure caused by predation is hypothesised to be the primary one responsible for the evolution of group life, defending a territory in order to secure food and mates from outgroup conspecifics represents two other key selective pressures in leading to social group living (van Schaik, 1983). The control over food resources is facilitated by a higher number of individuals participating in that task (Wrangham, 1980; Krebs & Davies, 1993) at least for certain species of primates, under specific conditions (Wrangham, 1987). Among primates the defence of food resources usually applies to females who forage socially for high quality food (fruits) and defend resources by displacing solitary females or smaller groups of females (Wrangham, 1980; Wich, Assink, Becher, & Sterck, 2002). In several primates, females represent a resource for males given their potential role as future mates (Trivers, 1972). As a consequence the control

males have over females can be direct, keeping away males of neighbouring groups, or indirect, through the defence of food resources which represent a more valuable source for females than for males (van Schaik, 1983, van Schaik, Assink, & Salafsky, 1992). For example, male colobus monkeys (*Colobus guereza*) defend female mates indirectly via resource control during intergroup encounters (Fashing, 2001). Another task males can carry out jointly is the protection of offspring from attacks of extra-group males (van Schaik, 1996, Steenbeek, Piek, van Buul & van Hoof, 1999). Indeed conflicts of reproductive interests can be expressed through infanticide, which are thought to increase males' reproductive success (Gibson, Vick, Palma, Carrasco, Taub, Ramos-Fernandez, 2008).

Aside from preventing infanticide, individuals in some species of social primates may cooperate in the rearing of offspring, which represents a further advantage of living in groups. Cooperative breeding is when individuals delay or forgo their own independent reproductive success to help other individuals, most often their relatives, to rear their young (Solomon & French, 1997). This breeding strategy is common among birds, some rodents and occurs among the callitrichid monkeys. In this latter case, most often maturing sons and daughters from a handful of breeding adults delay dispersal from the natal territory and assist their parents in rearing offspring. Help comes in the form of taking turns in carrying infants and provisioning them with food when they are mature enough to eat it (French, 1997; Schaffner & Caine, 2000).

Other selective pressures that might lead to group living have derived from cooperation between group members. Since many animals actively pursue common goals working together they attain benefits they could not attain alone; such as cooperative hunting in lions (Scheel & Packer, 1991) and in chimpanzees (Boesch, 1994; Mitani & Watts, 2001). In addition, group living is favoured by forms of mutualism in which individuals often of different species gain mutual benefits from an interaction (Lee, 1994) as demonstrated by the polyspecific associations in both new and old world primates (Waser, 1987) as well as in the process of information exchange, in which animals from the same community benefit from others about the location of food, availability and status of receptive females. A further advantage of group living is represented by thermoregulation,

which is crucial for individuals exposed to low temperatures and for small sized mammals (Lee, 1994). For example, sea lions (*Zalophus californianus)* huddled against one another at low temperatures (Gentry, 1973), and female Bechstein's bats (*Myotis bechsteinii)* roost in suitable group sizes to benefit from thermoregulation (Kerth & König, 1999).

1.1.2 Costs of group living

Despite the numerous advantages of group living, it also entails high costs. Even though the benefits of predator detection and avoidance are compelling, the more individuals are in a group, the greater the likelihood that individuals will be detected in the first place. The most direct cost of group living is feeding competition, in the form of reduced foraging efficiency (Terborgh & Janson, 1986). To satisfy the nutritional requirements of all the individuals in the group the foraging effort (travel and time) has to be adjusted to the number of individuals (Janson, 1988). The increase in time spent travelling is a cost associated with large group size. Furthermore, some individuals may be faster at removing limited food supplies from an area before other group members have a chance to feed (Janson & van Schaik, 1988) and experiments on wild populations of chacma baboons (*Papio ursinus*) demonstrate that for subordinate individuals this could be a regular occurrence (King, Douglas, Huchard, Issac & Colinshaw, 2008). It is further possible that individuals fight for the access to a limited resource with the consequent reduced food intake for some individuals. In wild capuchins contest over clumped feeding sites resulted in a four-fold food intake for dominants compared to subordinates (Janson, 1985)

A further cost entailed in group living is increased sexual competition. While mates do not need to be 'found' in group living animals, individuals have to cope with intra-sexual competition. As is the case for feeding resources, contest or scramble competition for mates depends on the distribution and availability of sexual resources (Radespiel, Ehresmann & Zimmermann, 2001). In primate species, where females produce gametes at a much lower rate than males, receptive females are a relatively scarce commodity and therefore competition among males is likely to arise (Trivers, 1972; Smuts, 1987). Interference

competition for mates includes all behavioural interactions between individuals of one sex that affect their access to mates, such as assessment, threat, fighting and deception (Terborgh & Janson, 1986). An extreme example of interference competition was reported for a community of chimpanzees where a lethal attack excluded one male's access to an estrous female (Fawcett & Muhumuza, 2000). Exploitation competition includes any behaviour that increases access to mates, except direct interactions with other individuals of the same sex (Wiley & Poston, 1996). For example, male mating success in ground squirrels (*Spermophilus tridecemlineatus*) depended on the ability to locate estrus females and not on the outcome of interactions between males (Schwagmeyer & Woontner, 1986).

To benefit from the joint exploitation of various activities some degree of group cohesion has to be maintained. Thus, individuals need to coordinate their activities to stay together. This means that some leader individuals will decide how to allocate the group's time among others, namely personal leadership (Leca, Gunst, Thierry & Petit, 2003; King & Colinshaw, 2009) or individuals make trade-offs to reach a collective decision to achieve some degree of self-organization (Conradt & Roper, 2005). Whatever the extent of leadership is, whether only adult males lead the group in gorillas (*Gorilla gorilla*, Schaller, 1963) or whether no specific leadership is associated with determined age, sex classes or dominance as in white faced capuchins (Leca, et al., 2003) and chacma baboons (Stueckle & Zinner, 2008), some individuals will experience a cost whenever their needs are not reflected by what was decided for the group. Furthermore, by affecting foraging efficiency increasing group size affects optimal allocation of time by every single individual when animals are forced to spend more time meeting basic needs and thus reduces the time allocated to other activities (Dunbar, 1992; Pollard & Blumstein, 2008).

A final and considerable cost to living in groups is that individuals are more exposed to the risk of being infected by pathogens or parasites compared to solitary individuals (Lee, 1994). Close proximity and contact as well as promiscuous mating are typical of social groups' behavioural repertoire and favour the spread of diseases (Altizer, Nunn, Thrall, Gittleman & Antonovics, et al.,

2003). Thus, the exposure to diseases represents a further cost of group living given its potential to spread rapidly over all group members (Freeland, 1976).

1.2. Conflicts of interest and aggression

Group life entails a continuos negotiation among objectives that cannot be carried out jointly or cannot be shared. Consequently, individuals are frequently exposed to conflicts of interests in which individuals within a group may want to pursue different activities or acheive different goals. When these conflicts cannot be resolved through other mechanisms, such as consensus decision making (Conradt & Roper, 2005), conflicts may degenerate into aggression. Aggression is defined as a "behaviour directed at members of the same species to cause physical injury or to warn of impending actions of this nature" (Aureli, Cords & van Schaik, 2002, p. 326). Traditionally, the term aggression was associated with a necessarily destructive behaviour and instead of viewing aggressive behaviour as a well integrated part of social relationships it was treated as a separate behavioural category isolated from other aspects of social life (de Waal, 2000b). It was commonly thought that aggression functioned to cause dispersal in all animals and thus decreased the probability of contact between opponents following aggressive interactions – the dispersal hypothesis (de Waal, 1993). Only recently a change in perspective of the concept of aggression shifted the attention from an "individual level", individual model of aggression, to a "social level" or relational model (de Waal, 2000a). In the individual model aggressive behaviour was relegated to a single individual's state, whereas in the relational model aggression figured as a functional tool within a social relationship where social bonds are based on a compromise between hostility and attraction, rather than on attraction alone (de Waal, 1986). In that sense "aggressive behaviour" is viewed as adaptative, as well as a necessary instrument to negotiate social relationships. Indeed, aggression is one way in which conflicts of interest are expressed and resolved (de Waal, 1993). Nevertheless, several negative consequences are entailed during and after aggressive interactions.

1.2.1 The consequences of aggression

The most direct effect of aggression is physical injury. Physical harm can range through varying degrees of intensity, ranging from superficial injuries to death. Athough rare, several species of primates engage in coalitionary aggression that leads to the death of group members (lion tamarins, *Leontopithecus rosalia*, Inglett, French, Simmons, & Vires, 1989; chimpanzees, Fawcett & Muhumuza, 2000; spider monkeys, *Ateles geoffroyi*, Campbell, 2006; Valero, Schaffner, Vick, Aureli & Ramos-Fernandez, 2006; muriquis, *Brachyteles arachnoides,* Talebi, Beltrão-Mendes, & Lee, 2009). A phenomenon called episodic targeting has been identified in captive and wild lemurs. Several species of lemurs engage in episodic targeting aggression whereby one or two individuals that have been group mates since birth or for several years are targeted for days or months by other group mates and often result in severe injury (Vick & Pereira, 1989). The involvement in an aggressive encounter is also likely to be highly costly in terms of energy consumed (Huntingford & Turner, 1987) and experimental studies testing this proposal in lizards and fish support this view (spiny lizards, *Sceloporus jarrovi*, Marler & Moore, 1989; amarillo fish, *Girardinichthys multiradiatus*, Valero, Hudson, Aliva Luna, & Macia Garcias, 2005). Furthermore, there is a risk associated with the visibility and audibility generated by a physical contest that can expose, not only the contestants, but the whole social group, to a higher predation risk (Lee, 1994). Moreover, recipients of aggression might lose access to specific ecological resources (Aureli, 1992). Long-tailed macaques (*M. fasicularis*) spent less time foraging after an aggressive encounter compared to control periods. Furthermore, aggressive events are associated with higher risk of renewed aggression. Indeed, in the aftermath of aggressive displays recipients of aggression are more likely to be re-targeted [patas monkeys, (*Erythrocebus patas*): York & Rowell, 1988; long-tailed macaques (*M. fascicularis*), Aureli & van schaik, 1991a; Aureli, 1992; Cords 1992; Das, Penke & van Hooff, 1998; Japanese macaques (*M. fuscata*), Schino, Rosati & Aureli, 1998; Kutsukake & Castles, 2001; baboons (*Papio cynocephalus ursinus*), Silk, Cheney & Seyfarth, 1996; (*P. anubis*), Castles & Whiten, 1998].

The uncertainty created by the potentially high risks entailed in aggressive interactions may create an altered emotional state in both former opponents. Self-directed behaviour (SDB), such as self-touch, self-grooming and scratching are

considered emotional indicators. Levels of SDB appear to be higher in situations of uncertainty, social tension, or impending danger (Maestripieri, Schino, Aureli & Troisi, 1992; Schino, Perretta, Taglioni, Monaco & Troisi, 1996). There is evidence that SDBs are elevated following aggressive interactions (Aureli & van Schaik, 1991; Castles & Whiten, 1998; Kusukake & Castles, 2001; Koski, Koops & Sterck 2007; Fraser, Stahl & Aureli, 2010). Although the anxious response in recipients of aggression is likely to be adaptive, as they are primed for action in the event of further attacks or more predisposed to behave submissively (Leshner, 1983), it can have negative physiological and developmental consequences over the long term (Honess & Marin, 2006).

1.3 Mechanisms to cope with aggression

Despite the negative effects of competition and aggressive conflicts, group living animals must have overcome the costs of aggression to gain the benefits of sociality. As a consequence animals living in stable social organisations are thought to have evolved specific behavioural mechanisms to deal with incompatibility over the same objectives. It can be argued that those mechanisms have been favoured through natural selection and are related to any given social and ecological environment of different species. Benefits of socialty and social cohesion can be maintained through the use of conflict management strategies. Conflict management includes all passive or active interventions at different critical stages of any non-compatible interest (goal) between two individuals. Conflicts of interest can indeed, be prevented, mitigated or the damage caused by aggressive escalation can be repaired (Aureli, et al., 2002).

1.3.1 Conflict prevention

Conflict prevention is one way to favour social stability without incurring in the costs related to escalation of aggression. Specifically, conflict prevention strategies are associated with increased social tension given its high potential for aggression (Judge, 2000). The pre-feeding context in provisioned groups is typically associated with an increase in social tension. The ability of provisioned animals to predict feeding time can produce a tension reduction response to reduce aggressive arousal before and during the forthcoming event (Koyama, 2000). As

reported for bonobos (*P. paniscus*, de Waal, 1987), rhesus monkeys (*M. mulatta*; de Waal, 1984), capuchin monkeys (*C. apella*, Polizzi di Sorrentino, Schino, Visalberghi, & Aureli, 2010) and chimpanzees (Koyama & Dunbar, 1996), grooming represents one way in which prefeeding tension is reduced, whereas bonobos increase rates of social play prior to feeding (Palagi, Paoli & Tarli, 2006). The increase in tension associated with pre-feeding is clearly related to contest competition that occurs when food is monopolisable. Indeed, only clumped and not dispersed distribution of the feeding resource yielded an increase of grooming behaviour in juvenile rhesus macaques (de Waal, 1984) and chimpanzees (Koyama & Dunbar, 1996). A further context typically associated with tension and potential for aggression is high density. Aggression is markedly increased among individuals under high density conditions as reported for non human primates (Judge, 2000). However, aggressive interactions are not the only response to increased density. Under high density a captive group of chimpanzees did engage more in aggressive behaviour compared to aggressive levels in the larger outdoor compound (Nieuwenhujisen & de Waal, 1982). Other studies reported a similar pattern of increased affiliative and submissive behaviour as an effect of greater densities (baboons: Rowell, 1967; Japanese macaque*s*, Alexander & Roth, 1971; bonobos, Sannen, Van Elsacker & Eens, 2004; Tacconi & Palagi, 2009). de Waal formulated a "coping model" suggesting that under high density conditions specific behaviours may be displayed to reduce tension and risk of aggressive escalation (de Waal, 1989). Conversely, as a result of increased denisty a number of studies provided evidence for an opposite trend, where aggressive behaviours were reduced under crowded conditions [rhesus macaques, (*M. mulatta*), Bercovitch & Lebron, 1991; chimpanzees, Aureli & de Waal, 1997]. The type of strategy adopted to cope with increased tension under high density can vary according to different species as well as the length of time individuals are exposed to high density (Judge, 2000). Short-term exposure to crowding might act as a constraint for the development of active behaviours functioning in reducing social tension. Inhibition of aggression is the most effective strategy in the short term (de Waal, 1989). Comparison of density effects in the long and short-term provide evidence for such a temporal effect on the coping strategies adopted (rhesus monkeys, Judge & de Waal, 1997; chimpanzees, Videan & Frits, 2007).

Dominance is another mechanism that mitigates and prevents aggressive escalation (de Waal 1986; de Waal & Luttrell, 1989; Preuschoft & van Schaik, 2000). In animals that experience high contest competition over resources power asymmetries arise, and when there is an imbalance of power between potential opponents the outcome from aggressive conflicts is predictable. Under these circumstances despotic dominance hierarchies are likely to arise to circumvent aggression, and in turn submission is formalised by unidirectional displays used by subordinates, which saves them energy because they avoid overt aggression (de Waal, 1986; Preuschoft & van Schaik, 2000). For example, subordinate rhesus macaques typically display the "silent bared-teeth" to dominant individuals to gain access to social sites or partners (de Waal & Luttrell, 1985; Preuschoft, Gevers & van Hooff, 1995). By contrast, when power is more balanced (tolerant dominance) conflict outcome is less predictable and dominants might induce submission through the use of formal threat signals. Such communication of power asymmetries defines a priority in the access over limited resources that favours a rather peaceful coexistence among group members. For example tolerant male crested black macaques (*M. nigra*) signal dominance status with loud calls. Such vocal displays are a means to prevent contests between males for mates (Neumann, Assahad, Hammerschmidt, Perwitasari-Farajallah & Engelhardt, 2010).

Greeting gestures represent a further pre-emptive means of conflict avoidance and prevention. Affiliative behaviours are displayed by a variety of species in a reunion context. Greeting displays have been reported for non human primates and other mammals and fishes [capuchin monkeys, Manson, Perry & Parish, 1997; chimpanzees, Bauer, 1979; Nishida, Kano, Goodall, McGrew, & Nakumara, 1999; Okamoto, Agetsuma, &Kojima, 2001; spider monkeys, Klein & Klein 1971; Schaffner & Aureli, 2005; Aureli & Schaffner, 2007; spotted hyenas, *Crocuta crucuta*, East, Hofer & Wickler, 1993; sea horses (*Hippocampus whitei*), Vincent, 1995; butterflyfish (*Chaetodon lunulatus*),Yabuta, 2002]. These greeting behaviours are species-specific and may serve different functions, ranging from needing to identify each other (Yabuta, 2002), to test bonds (Zahavi, 1977), and to reassure one another about intentions (Schaffner & Aureli, 2005; Aureli & Schaffner, 2007). Thus, species that are frequently dealing with high tension

during the reunion context are more likely to have evolved behavioural mechanisms that reduce the likelihood of aggressive escalation.

1.3.2 Conflict resolution and reconciliation

Much greater research attention has been given to post conflict mechanisms that serve to repair damage to relationships in the aftermath of aggressive behaviours. Conflict resolution is defined as the "outcome of actions that eliminate the incompatibility of goals, interests or attitudes of the conflicting individuals" (Aureli, Cords & van Schaik, 2002, p. 326). Thus, after a conflict resolution there might still be some incompatibility among a specific objective, but the pattern of interaction between two former opponents is at least partially restored. Reconciliation is the most basic conflict resolution mechanism and is defined as a post-conflict friendly reunion of the former opponents (de Waal & van Roosmalen 1979). Reconciliation was discovered when, in contrast with the common view, chimpanzees were attracted instead of dispersed after being involved in aggressive conflicts (de Waal & van Roosmalen, 1979). Following de Waal and van Roosmalen's pioneering study, reconciliation was demonstrated in the vast majority of the studies conducted on non human primates and other animals (Table 1.1)

Currently, there are predominantly two key hypotheses for the function of reconciliation: the valuable relationship hypothesis and the uncertainty reduction hypothesis (Arnold & Aureli, 2007). The most relevant and widely demonstrated is the valuable relationship hypothesis, which states that conflicts between individuals that share a beneficial relationship are more likely to be reconciled (de Waal & Aureli, 1996; Aureli et al., 2002). For example, aggressive interactions among kin are reconciled more frequently than those between non-kin as a function of the benefits that can be derived from such relationships (Aureli , et al., 1989; Veenema, Das & Aureli, 1994; Castles, Aureli & de Waal, 1996; Aureli, Das & Veenema, 1997; Schino, Rosati & Aureli, 1998). However, kinship is not the only determinant of valuable relationships. A number of studies have provided a more detailed definition of relationship quality depending on the species studied. Relationship value has also been measured through the degree of affiliative behaviour, agonistic support and cooperative behaviours exchanged between

partners (see Chapter 3). Subsequently, the influence of valuable relationship on reconciliation has been the subject of a number of studies, which largely provided evidence for the valuable relationship hypothesis (Table 1.1).

On a more proximate level, reconciliation may serve to reduce post-conflict anxiety and return SDBs to their pre-conflict levels. It has been suggested that the increased levels of anxiety are due to the uncertainty about the post-conflict situation, and reconciliation reduces such uncertainty (the uncertainty reduction hypothesis: Aureli, van Schaik & van Hooff, 1989; Aureli & van Schaik, 1991). In many species, not only victims, but also aggressors experience an increase in SDB in the aftermath of a conflict (Aureli, 1997; Das, et al., 1998; Romero, Colmenares & Aureli, 2009). Given that anxiety following aggression affects both victims and aggressors it has been proposed that the damage brought about by agonistic interactions concerns the relationship of the former contestants (Aureli & van Schaik, 1991a). Elevated levels of anxiety are likely to mediate the occurrence of reconciliation, so that higher rates of SDBs result as a proximate mechanism regulating behavioural responses of the opponents. There is evidence supporting this view as higher SDB rates occur after conflicts between valuable partners which are also more likely to reconcile (Aureli, 1997; Kutsukake & Castles, 2001; Koski et al., 2007a). Due to the interdependency between the valuable relationship hypothesis and the uncertainty reduction hypothesis the integrated hypothesis has been proposed to account for both these perspectives (Aureli, 1997).

A predictive framework outlining rules about whether reconciliation should occur between former opponents was presented by Aureli et al. (2002). The specified conditions for reconciliation include that species recognise the conspecifics in their social groups; that aggressive interactions occur between individuals living in social groups, because individuals that do not resolve conflicts of interest with aggression (e.g., avoidance of the opponent) would not need to repair their relationships; and that after aggression the relationship between former opponents is disturbed, either through reduced tolerance, increased risk of renewed attack, or loss of cooperation or a combination of these.

Table 1.1 Reconciliation Studies

Source	Species	Location	Reconciliation	Consolation (third party affiliation with victim)	Reconciliation during feeding	Post-conflict increase in self directed behaviours (SDB)	Effect of reconciliation on self directed behaviours (SDB)	Effects of variables defining quality of relationships on reconciliation	Degree of social cohesion and fission-fusion dynamics (ff)
Prosimians									
Kappeler, 1993	Ring tailed lemurs (*Lemur catta*)	captivity	no	no					
Rolland & Roeder, 2000	"	captivity	yes	no					
Palagi, Paoli & Borgognini Tarli, 2005	"	captivity	yes						
Kappeler, 1993	Red fronted lemurs (*Eulemur fulvus*)	captivity	yes	no				yes (kinship) more	
Roeder, Fornasieri & Gosset, 2002	Brown lemur (*Eulemur fulvus*)	captivity	yes						
Roeder, Fornasieri & Gosset, 2002	Black lemur (*Eulemur macao*)	captivity	no						
Palagi, Antonacci & Norscia, 2008	Sifaka (*Propithecus verreauxi*)	wild	yes		yes			yes value (contact, grooming friendly interactions) more	low
New World monkeys									
Westlund, Ljungberg, Borefelt, Abrahamsson, 2000	Common marmosets (*Callithrix jacchus*)	captivity	yes						low
Peňate, Peláez, & Sanchez, 2009	Cotton-top tamarins (*Saguinus oedipus*)	captivity	yes					male-male only	
Verbeek & de Waal, 1997	Brown capuchins (*Cebus apella*)	captivity	yes	no	yes				
Weaver & de Waal, 2003	"	captivity	yes			yes		yes mother-offspring security, more	
Daniel, Santos & Cruz, 2009	"	captivity	yes		no		victims	yes values (agonsitic support); no compatibility(counter intervention)	
Leca, Fornasieri & Petit, 2002	White faced capuchins (*Cebus capucinus*)	captivity	yes					Male-female only	

Table 1.1 Continued

Source	Species	Location	Reconciliation	Consolation (third party affiliation with victim)	Reconciliation during feeding	Post-conflict increase in self directed behaviours (SDB)	Effect of reconciliation on self directed behaviours (SDB)	Effects of variables defining quality of relationships on reconciliation	Degree of social cohesion and fission-fusion dynamics (ff)
Pereira, Schill & Charles, 2000	Guayanese squirrel monkeys (*Saimiri sciureus*)	captivity	yes					yes (proximity) more	
Schaffner, Aureli & Caine, 2005	Red-bellied tamarins (*Saimiri labiatus*)	captivity	no						
Old World monkeys									
Cheney & Seyfarth, 1989	Vervet monkeys (*Cercopithecus aethiops*)	wild	yes					no (kin)	
York & Rowell, 1988	Patas monkeys (*Erythrocebus patas*)	captivity	yes					yes (matrilineal kin)	
Gust & Gordon, 1993	Sooty managbeys (*Cercocebus torquatus atys*)	captivity	yes					no (kinship)	
Cooper & Bernstein, 2002	Assamese macaques (*Macaca assamensis*)	wild	yes					yes (MM and FF >FM	
Cooper, Bernstein & Hemelrijk, 2005	"	wild	yes					yes :females, value (grooming and aiding) more, no: males, value	
de Waal & Ren, 1988	Stumptailed macaques (*Macaca arctoides*)	captivity	yes					no (contact)	
Call, 1999	"	captivity	yes						
Cords, 1988	Long-tailed macaques (*Macaca fascicularis*)	captivity	yes					yes: immature males (kinships)	low
Das, Penke & van Hooff, 1998	"	captivity	yes			aggressor	aggressor		low
Aureli, van Schaik & van Hooff, 1989	"	captivity	yes				victims	yes (kinship and valuable relationships (affiliative contact)	low
Aureli, 1992	"	wild	yes	no	yes	victims			low
Cords, 1992	"	captivity	yes					tolerance	low
Aureli, Veenema, van Panthaleon van Eck & van Hooff, 1993	Japanese macaques (*Macaca fuscata*)	captivity	yes	no					low
Petit, Abegg & Thierry, 1997	"	captivity	yes						low

Table 1.1 Continued

Source	Species	Location	Reconciliation	Consolation (third party affiliation with victim)	Reconciliation during feeding	Post-conflict increase in self directed behaviours (SDB)	Effect of reconciliation on self directed behaviours (SDB)	Effects of variables defining quality of relationships on reconciliation	Degree of social cohesion and fission-fusion dynamics (ff)
Schino, Rosati & Aureli, 1998	"	captivity	yes					yes (kinship) and (grooming) more	low
Koyama, 2001	"	wild	yes		yes				low
Kutsukake & Castles, 2001	"	wild	yes			victims of kin opponent		yes	low
Abegg, Petit & Thierry, 2003	"	captivity	yes						low
Majolo, Ventura & Koyama, 2009	"	wild	yes					yes (grooming) more	low
Matsumara 1996	Moor macaques (*Macaca maurus*)	captivity	yes						
Call, 1999	Rhesus (*Macaca mulatta*)								
Demaria & Thierry, 2001	"	captivity	yes						
de Waal & Yoshihara, 1983	"	captivity	yes					yes (kinship)	
de Waal & Ren, 1988	"	captivity	yes						
Call, Judge & de Waal, 1996	"	captivity	yes					yes (kinship)	
Judge, 1991	Pigtail macaque (*Macaca nemestrina*)	captivity	yes						
Abegg, Thierry & Kaumanns, 1996	Lion-tailed macaques (*Macac silenus*)	captivity	yes						
Patzelt, Pirow & Fischer, 2009	Barbary macaques (*Macaca sylvanus*)	captivity	yes					yes females: value (sociopositive contact and support)	
Berman, Ionica, Dorner & Li, 2006	Tibetan macaques (*Macaca tibetana*)	wild	yes					No (tolerance levels and agonistic support)	
Demaria & Thierry, 2001	Tonkean macaques (*Macaca tonkeana*).	captivity	yes						
Swedell, 1997	Gelada baboon (*Theropithecus gelada*)	captivity	yes						
Castles & Whiten, 1998	Olive baboons (*Papio anubis*)	wild	yes					yes (kinship)	
Silk, Cheney & Seyfarth, 1996	Baboons (*Papio cynocephalus*)	wild	yes					no (kinship)	

Table 1.1 Continued

Source	Species	Location	Reconciliation	Consolation (third party affiliation with victim)	Reconciliation during feeding	Post-conflict increase in self directed behaviours (SDB)	Effect of reconciliation on self directed behaviours (SDB)	Effects of variables defining quality of relationships on reconciliation	Degree of social cohesion and fission-fusion dynamics (ff)
Romero, Colmenares & Aureli, 2009	Hamadryas baboons (*P. hamadryas*)	captivity	yes			aggressor (increasing in valuable partners)	aggressor		low
Petit & Thierry, 1994	Guinea baboons (*Papio papio*)	captivity	yes						
Sommer, Denham & Little, 2002	Langurs (*Presbytis entellus*)	wild	no						
Ren, Yan, Su, Qi, Liang et al. 1991	Golden monkeys (*Rhinopithecus roxellanae*)	captivity	yes						
Arnold & Barton, 2001	Spectacled leaf monkey(*Trachypitecus obscurus*)	captivity	yes					yes (grooming, body contact and huddling), no kinship	
Bjornsdotter, Larsson & Ljungberg, 2000	Black and white guereza (*Colobus guereza*)	captivity	yes						
Great apes									
Watts, 1995	Gorilla (*Gorilla beringei*)	wild	yes					yes (male-female)	
Cordoni, Palagi & Borgognini Tarli, 2006	"	captivity	yes					yes: value (female-male) only	
Homann & Fruth, 2000	Bonobos (*Pan paniscus*)	wild	yes						ff
Palagi, Paoli & Borgognini Tarli, 2004	"	captivity	yes					yes friendship (grooming and contact sitting)	ff
de Waal, 1987	"	captivity	yes					yes (female-female)	
de Waal & van Roosmalen, 1979	Chimpanzees (*Pan troglodytes*)	captivity	yes						ff
Arnold & Whiten, 2001	"	wild	yes	no				yes compatibility (contact, grooming & proximity)	ff
Fuentes, Malone, Sanz, Matheson & Vaughan, 2002	"	captivity	yes	no					ff
Preuschoft, Wang, Aureli & de Waal,	"	captivity	yes					yes (grooming) no (support)	ff

Table 1.1 Continued

Source	Species	Location	Reconciliation	Consolation (third party affiliation with victim)	Reconciliation during feeding	Post-conflict increase in self directed behaviours (SDB)	Effect of reconciliation on self directed behaviours (SDB)	Effects of variables defining quality of relationships on reconciliation	Degree of social cohesion and fission-fusion dynamics (ff)
Wittig & Boesch, 2003	"	wild	yes	yes				yes value (mating partners)	ff
Kutsukake & Castles, 2004	"	wild	yes	yes				no (sex combination and association levels)	ff
Wittig & Boesch, 2005	"	wild	yes					yes value (food sharing and support)	ff
Koski, de Vries, van den Tweel & Sterck, 2007	"	captivity	yes	yes				yes values (F-M mating benefits)	ff
Koski, Koops & Sterck 2007	"	captivity	yes			higher in victims of valuable dyads	no	yes value (M-M) yes compatibility (grooming)	ff
Fraser & Aureli, 2008	"	captivity	yes	yes				yes value (food sharing, agonistic support and grooming)	ff
Fraser, Stahl & Aureli, 2010	"	captivity	yes				yes	yes (female-female) and value	ff
Non primate mammals									
Cools, van Hout & Nelissen, 2008	Domestic dogs (*Canis familiaris*)	captivity	yes	yes				yes (familiarity-same housing)	
Cordoni& Palagi, 2008	Wolves (*Canis lupus*)	captivity	yes					yes (support), no (body contact)	
Schino, 1998	Domestic goat (*Capra hircus*)	captivity	yes				victim (no aggressor)		
Wahaj, Guse & Holekamp, 2001	Spotted hyena (*Crocuta crocuta*)	wild	yes					no (kinship)	ff
van den Bos, 1998	Cats (*Felis silvestris*)	captivity	no			yes			
Kutsukake & Clutton-Brock, 2008	Meerkats (*Suricata suricatta*)	wild	no						
Samuel & Flaherty, 2000	Bottlenose dolphin (*Tursiops truncatus*)	captivity	yes						ff
Birds									
Seed, Clayton & Emery, 2007	Rooks (*Corvus frugilegus*)	captivity	no	yes					

Even if species meet all the conditions they will not necessarily reconcile, unless there is a loss of benefits. Therefore, rules were also proposed to predict when reconciliation should occur (Aureli et al. 2002). Rule 1 states reconciliation should occur when the benefits of signalling the end of the conflict are greater than the costs of further aggression from the former opponent. Rule 2 states reconciliation should occur when aggression undermines relationships that are mutually valuable and it should occur more when relationships are more valuable.

1.3.3 Post conflict bystander affiliation

Other individuals apart from the opponents can be actively involved in post-conflict interactions. de Waal and van Roosmalen (1979) noted that recipients of aggression were often involved in affiliative interactions with a bystander. They defined that behaviour as consolation. However, bystander affiliative interactions differ greatly whether the recipient of aggression or the bystander is the initiator. Indeed, the bystander exposes him or herself to high a risk of aggression when he or she initiates affiliative interactions with the receiver of aggression, termed consolation, whereas bystanders incur no risk when affiliative interactions are solicited by the recipient of aggression, termed solicited affiliation (Fraser, Koski, Wittig & Aureli, 2009). So far, bystander affiliation has been demonstrated on a few species of non- human primates, domestic dogs (*Canis familiaris*) and rooks (*Corvus frugileus*) (Table 1.1).

Several functions have been proposed for bystander affiliation. It is thought to serve as appeasement and stress reduction for the recipient of aggression (de Waal & van Roosmalen, 1979; Aureli, 1997). It has been proposed that when reconciliation does not occur bystander affiliation might work as a substitute mechanism to reduce stress especially when approaching the former aggressor is too risky (Wittig & Boesch, 2003). The self-protection hypothesis proposes that bystanders direct affiliative interactions to the recipient of aggression to avoid being targeted via redirected aggression. Indeed, a study conducted on chimpanzees provided evidence that opponents received third party affiliation most often when they were more likely to redirect aggression to third parties (Koski, de Vries, van den Tweel & Sterck, 2007). A study on stumptailed macaques showed how unsolicited affiliation occurred using socio-sexual behaviours (Call, Aureli & de Waal, 2002). Stumptailed macaques are so far the only species of monkeys to engage in unsolicited affiliation. According to

the cognitive constraint hypothesis stumptailed macaques lack the emotional mediation that is thought to drive consolation in the great apes (de Waal & Aureli, 1996). Thus, it seems that in different species the risk of aggression for bystanders on approaching the recipient of aggression influences the occurrence of unsolicited affiliation (de Waal & Aureli, 1996). Therefore, the function of unsolicited affiliation may vary among different species with different levels of social tolerance (Fraser, et al., 2009).

1.4 Fission-fusion dynamics

Social animals must continuously balance the trade-off between the costs and benefits of group living. One mechanism to manage this trade-off is to vary the degree of cohesiveness among group mates. The degree of spatio-temporal cohesiveness can vary between and within species (Kappeler & van Schaik, 2002; Aureli et al., 2008). Species with a high degree of fission-fusion dynamics (FF dynamics) live in communities that constantly split and merge into subgroups of varying size and composition (McFarland, 1986; Aureli, Schaffner, Boesch, Bearder, Call et al., 2008). The abundance and distribution of food resources is thought to have favoured the evolution of social organisations with a high degree of fission-fusion (Kummer, 1971; Chapman, 1990, Couzin, 2006). Another factor that contributed to the selection of species with high FF dynamics is the different costs of group living for each community member (Chapman, 1990). A recent model representing the degree of fission –fusion dynamics in a three dimensional framework highlights a rather flexible aspect of FF dynamics due to direct responses to fluctuation in predation pressure and food availability (Aureli, et al., 2008). Thus, societies can be viewed as dynamic entities encompassing multiple scales of organisation. Among primates, fluid FF dynamics, where individuals are rarely all together, have been identified in bonobos (Nishida & Hiraiwa-Hasegawa, 1987), chimpanzees (Mitani, Watts & Muller, 2002) , spider monkeys (*Ateles* spp., Symington, 1990; Wallace, 2008; Aureli & Schaffner, 2008), muriquis (Milton, 1984), ruffed lemurs (*Varecia rubra*, Vasey, 2006) and uakaris (*Cacajao* spp, Bowler & Bodmer, 2009). Other primate species perform FF dynamics characterised by a more rigid structure of subgroup size and composition, such as a long time spent solitary or in rather fixed subgroups where the smallest subgroup composition is

always comprised of the same individuals, such as the one male units of hamadryas baboons (*Papio hamadryas*, Stammbach, 1987). In other mammals social organisations characterised by high FF dynamics are typical of dolphins (*Tursiops* spp, Smolker, Richards, Connor & Pepper, 1992), spotted hyenas (Hofer & East, 2000), elephants, (*Loxodonta* spp., Poole & Moss, 2008), bats (Popa-Lisseanu, Bontadina, Mora & Ibañez, 2008), African buffalos (*Syncerus caffer*, Cross, Lloyd-Smith & Getz, 2005), lions (Packer, Scheel & Pussey, 1990) and red deer (*Cervus elaphus*, Albon, Staines, Guinness & Clutton-Brock, 1992).

1.4.1 Spider monkeys

The Yucatecan spider monkey (*A. geoffroyi yucanensis*) is the focus of my research. Spider monkeys' FF dynamics are characterised by a stable social unit, defined as community, whose individuals split in small non-permanent subgroups (McFarland, 1986), which can change in membership from day- to- day or from hour-to-hour (McFarland, 1986; Symington, 1990). Subgroups are often sex-segregated in that adult females and their dependent offspring frequently travel and forage independently of the community's adult males (Fedigan & Baxter, 1984; Ahumada, 1989). Patterns of fission-fusion vary according to the abundance and resource distribution to reduce direct feeding competition and travel distance (Di Fiore & Campbell, 2007; Asensio, Korstjens, & Aureli, 2009). Intra-group contest competition is also reduced by FF dynamics adjusting the subgroups size to the overall food availability in the community home range (Asensio, Korstjens, Schaffner, & Aureli, 2008). In sum, FF dynamics create opportunities for individuals to flexibly respond to variations in ecological and social factors. Therefore, the role played by FF dynamics is likely to be relevant in characterising the nature of conflict management as it provides a wider spectrum of options compared to more cohesive social units. However, little is known about the effect of varying degrees of fission-fusion on the mechanisms to regulate conflicts.

1.4.2 Conflicts of interest and FF dynamics

In social animals important decisions need to be taken jointly with other group members to maintain group cohesion. The combined decision usually affects

the group as a whole. Conflicts of interest are likely to arise when the decision is not favourable for a few group members (Conradt & Roper, 2005). However, animals living in communities with high FF dynamics are provided with the option to avoid such conflicts of interest by temporarily splitting into subgroups when reaching a consensus decision among all community members is not in their favour (Kerth, Ebert & Schmidtke, 2006). The modality and influence of FF dynamics on group decisions was studied in female Bechstein bats, which live in colonies consisting of multiple subgroups that change during frequent roost switching (Kerth & König, 1999). This switching implies that colony members must regularly make group decisions over where to roost. When individuals were provided with conflicting information about the suitability of potential roosts, group decisions reflected the information available to the majority of individuals. However, conflicting information led to an increased fission suggesting that FF dynamics allow individuals to opportunistically split from the subgroup when the group decision is not the best outcome (Kerth, et al., 2006). Further evidence of fissioning as a possible strategy in response to unfavourable despotic group decisions is provided by an experimental study conducted on chacma baboons (King, et al., 2008). Although chacma baboons do not show high fluidity in subgroup composition on a daily basis, they may occasionally form temporary subgroups (Aureli et al., 2008 supp. B). Group decision in this species was consistently taken by dominant individuals, who acquired the greatest benefit from those decisions, and were followed by subordinate members. However, subordinates were found to fission from the group when relationships with the leader were weak, suggesting the costs were too high.

Communicative abilities represent one more interesting implication in animals living in communities with high FF dynamics. Communicative displays may have evolved in a more extensive and sophisticated repertoire in species living with a high FF dynamics compared to those living with lower FF dynamics (Aureli et al., 2008). Uncertainties about relationships in the face of frequent separation need to be resolved and at fusion events greeting displays may be used to signal good intentions. Specific behavioural displays are used during reunions (chimpanzees, Bygott, 1979; Nishida, et al. 1999; Okamoto, Agetsuma, & Kojima, 2001; spider monkeys, Klein & Klein 1971; Schaffner & Aureli, 2005; Aureli & Schaffner, 2007; hamadryas baboons, Colmenares, Hofer & East, 2000; spotted hyenas: East, et al.,

1993). Additionally, individuals may use vocal signals to keep track of group members ranging in separate subgroups, to coordinate their activities or to communicate important information such as food availability or presence of predators. Several species living in communities with high FF dynamics are capable of recognising familiar individuals through vocalisations or whistles (chimpanzees, Herbinger, Papworth, Boesch & Zuberbuehler, 2009; spider monkeys, Teixidior & Byrne, 1999; Ramos-Fernandez, 2005; elephants, McComb, Moss, Sayialel & Baker, 2000; spotted hyenas, Holekamp, Boydston, Szykman, Graham, Nutt, et al., 1999; dolphins, Sayigh, Tyack, Wells, Solow, Scott & Irvine, 1999). These communicative displays might play a role in keeping individuals in contact when ranging in separate subgroups. The function of such signals may be as conflict prevention mechanisms reducing social tension at fusion events (Schaffner & Aureli, 2005; Aureli & Schaffner, 2007). Moreover, it is possible that the ability to recognise individuals using vocal signals provides individuals with the option to avoid encountering group members with whom a high potential for aggression exists.

Living in communities with high FF dynamics may influence individuals' social relationships given the different opportunities community members have to interact with one another (Aureli & Schaffner, 2008). Non-random association patterns can arise for two reasons (Kerth & König, 1999): 1) individuals sharing common preferences or needs tend to aggregate in specific locations; or 2) individuals actively seek association with specific partners, with whom to cooperate. For example, spider monkeys and chimpanzees form all-male subgroups actively cooperating in territorial defence from neighbouring groups (Shimooka, 2003; Aureli, Schaffner, Verpooten, Slater, & Ramos-Fernandez, 2006; Wallace, 2008; Watts, 1998). Female Bechstein's bats associate in communal roosts depending on their reproductive status: lactating females preferentially roost together to cooperate with one another in tasks such as mutual warming of pups, guarding of juveniles and communal nursing (Kerth & König, 1999).

Given then the most important factors influencing spider monkeys' ranging and association patterns are the availability and distribution of high quality food (McFarland, 1986; Chapman, 1990; Wallace, 2008; Asensio et al., 2009), environmental changes affecting these factors are expected to have a direct impact on

spider monkeys' behaviour. The modality in which such changes influence the diet, activity and subgrouping patterns can provide insight on the flexibility of spider monkeys' behavioural repertoire. The occurrence of two hurricanes in the middle of the data collection of the present study revealed how the monkeys used behavioural mechanisms to adapt to the disturbed environment. Particular attention was given to the role of fission-fusion dynamics as conflict management strategies.

1.5 Aims of the thesis

In the present series of studies I aimed to investigate the mechanisms that regulate the management of conflicts in two communities of wild spider monkeys. Spider monkeys were an excellent species in which to investigate this topic area as they are relatively understudied with respect to social dynamics (Aureli & Schaffner, 2008) and there are no published studies of reconciliation on this taxon. Even though, post-conflict management mechanisms have been investigated for over three decades, since de Waal and van Roosemalen (1979), there has been no systematic study of pre-conflict management mechanisms in any species, a shortcoming that has been pointed out previously by Aureli et al., (2002). Finally, several studies have demonstrated that the quality of social relationships influences the occurrence of conflict management mechanisms (Cords & Aureli, 2000; Watts, 2006; Arnold & Aureli, 2007) and therefore it was important to ascertain a reliable approach and subsequent measure of the quality of the social relationships among the spider monkeys.

The first aim of my study was to examine the quality of relationships in spider monkeys. Relationship quality is a key factor in determining conciliatory tendencies. The nature of the opponents' relationship is important in evaluating the benefits and costs of post-conflict interactions. Specifically, conciliatory tendencies are expected to increase when dyadic relationships are more valuable, less secure and highly compatible (Cords & Aureli, 2008). Animals living in social groups are likely to form long-lasting individualised relationships and this is very likely to hold for spider monkeys which are among the longest-living monkeys species, regularly exceeding the age of 40 in captivity (Shimooka et al. 2008) and they have a long inter-birth interval of three years (Vick, 2008). Spider monkeys are therefore suitable subjects for the understanding of the influence of social relationships on behavioural

mechanisms to prevent and repair aggressive escalation. There is little consistency, however, in how the quality of relationships has been studied previously. Cords and Aureli (2000) identified three components of relationship quality and proposed behavioural measures to define such components with the goal to reduce the discrepancy among the existing definitions and assessments. In my study, I aimed to identify components of relationship quality that regulate spider monkeys' dyadic interactions through the use of a novel, more objective method. In Chapter 3 I used a number of behavioural measures in a principal components analysis to assess the relative importance of each measures and their categorisation within the components. Furthermore, I aimed to analyse the influence categorical variables such as age, sex, tenure and kinship had on the components obtained.

The second aim of my study was to examine post-conflict management mechanisms in wild spider monkeys, which are explored in Chapter 4. Despite the vast number of studies examining the use of post-conflict reconciliation on a large number of non-human primates, no attempt has yet been made to determine whether spider monkeys engage in reconciliation or any other post-conflict interaction. This entailed first determining the pattern and frequency of aggression among the spider monkeys in the two communities, followed by systematically examining whether reconciliation, bystander intervention or redirected aggression occurred in the aftermath of aggressive conflicts. Furthermore, I attempted to broaden the understanding of spider monkeys' conflict management mechanisms by analysing the effect components of relationship had on the behavioural strategy employed. Although several studies exist on post-conflict interactions on societies characterised by high FF dynamics, no information is yet available on how such low cohesiveness affects conflict management. The prediction that animals living in less cohesive societies could exploit the option to temporarily leave the subgroup of membership in the aftermath of aggression is more viable for animals living in less cohesive societies (Schino, 2000, Aureli et al, 2008), and has never been systematically tested. Thus, I introduced subgroup fission as possible outcome of post-conflict behaviour to examine whether former opponents avoid each other after aggressive interactions.

In animals living in communities characterised by high FF dynamics, fusion events are probably filled with uncertainty as individuals may have been separated

for several days and therefore social tension among individuals joining together is likely to characterise fusion event. Indeed, aggressive escalation is likely to occur in the reunion context as reported for chimpanzees (Bauer, 1979; Bygott, 1979; Goodall, 1989) and spider monkeys (Klein & Klein, 1971; Aureli & Schaffner, 2007). However, despite the opportunity fusion events offer to investigate mechanisms of conflict prevention, very little attention has been given to such episodes. So far, the only studies performed on conflict management at fusion events were conducted on spider monkeys and provided evidence for affiliative behaviours actingas a mechanism for tension reduction and appeasement among individuals (Schaffner & Aureli, 2005; Aureli & Schaffner, 2007). Therefore, in Chapter 5 I aimed to examine the role of friendly and aggressive behaviour in the aftermath of fusion events to understand the modality in which conflict prevention mechanisms are adopted. The latencies in which aggressive and friendly behaviours are performed after fusion events should shed light on the temporal variations at which these behaviours are exhibited and might reveal patterns of interdependency. Furthermore, I explored the possible functions of the friendly behaviours in the aftermath of fusion, whether the behaviours serve to signal benign intent, provide a mechanism for testing bonds between individuals that had been separated or whether such signals merely function as means of recognition between conspecifics from the same community. Finally, I aimed to analyse the influence components of relationships have on the latencies of aggressive and friendly behaviours.

In Chapter 6, I present the effects a natural disaster had on the ecology and behaviour of the two communities I studied. Hurricanes can cause severe damage to the forest structure. Only a few detailed studies on the effect of cyclonic storms are available for non-human primates. The occurrence of two hurricanes only three months apart affected my research project by impacting on the activity budgets and FF dynamics of the two spider monkey communities. The availability of pre and post hurricane observations provided me with the opportunity to examine spider monkeys' behavioural flexibility in a disturbed habitat. The focus of this chapter was to examine how reduced food resources affected the conflict management strategies in wild spider monkeys. Specifically, I examined mechanisms that served to prevent aggressive conflicts. Given that variation in food supply in spider monkeys affects their dispersion and association patterns I explored the subgroup dynamics of the

monkeys in two temporal comparisons before and after the hurricane. The adjustment of subgroup size to the food availability reduces the risk of increased feeding competition and represents therefore a preventive mechanism to avoid conflict of interests. The rate of fusion events reflects how frequently individuals join other individuals thereby increasing their subgroup size and provides another measure to detect conflict prevention mechanisms. The potential for feeding competition is higher in larger subgroups especially in association with reduced food availability. In addition, fusion events have a high potential for aggression. Thus a change in fusion rates might reflect a strategy to avoid aggressive escalation especially in a disturbed environment where conflicts of intereset are more likely to arise and where individuals need to save their energy.

Chapter 2

General Methodology

2.1 Study site

The study site is located in the Yucatán Peninsula, Mexico, state of Yucatán, adjacent to the Mayan village of Punta Laguna (20°38' N, 87°38' W, 14m elevation). The study area has been promoted to a Natural Protected Area (NPA) in 2002, and named *Otoch Ma'ax Yetel Kooh (the monkey's and puma's house)*. The climate is tropical sub-humid with a dry season ranging from approximately November to April and a wet season during the rest of the year. Hurricanes are likely to form during the months from June to November. During the years of my field data collection (2005, 2006), the mean annual temperature was of 26.6°C with a minimum of 9°C and a maximum of 37°C. The mean daily rainfall was 4.56 mm in 2005 and 4.0 mm in 2006 (Estación Climatológica del Ideal; CNA).

The NPA has an area of 5,367 hectares and includes varying degrees of regenerating forest. Approximately, 700 hectares are occupied by old growth medium semi-deciduous forest, whereas the majority of the area, about 2700 hectares, consists of 30-50 year old successional forest (Figure 2.1). The local inhabitants previously exploited the land through the use of slash and burn agriculture to support themselves with the cultivation of corn. A very small portion of the area is still used for this purpose; however, since the foundation of Punta Laguna, in the late 1930s, the same villagers preserved the forest, which eventually was declared part of the NPA.

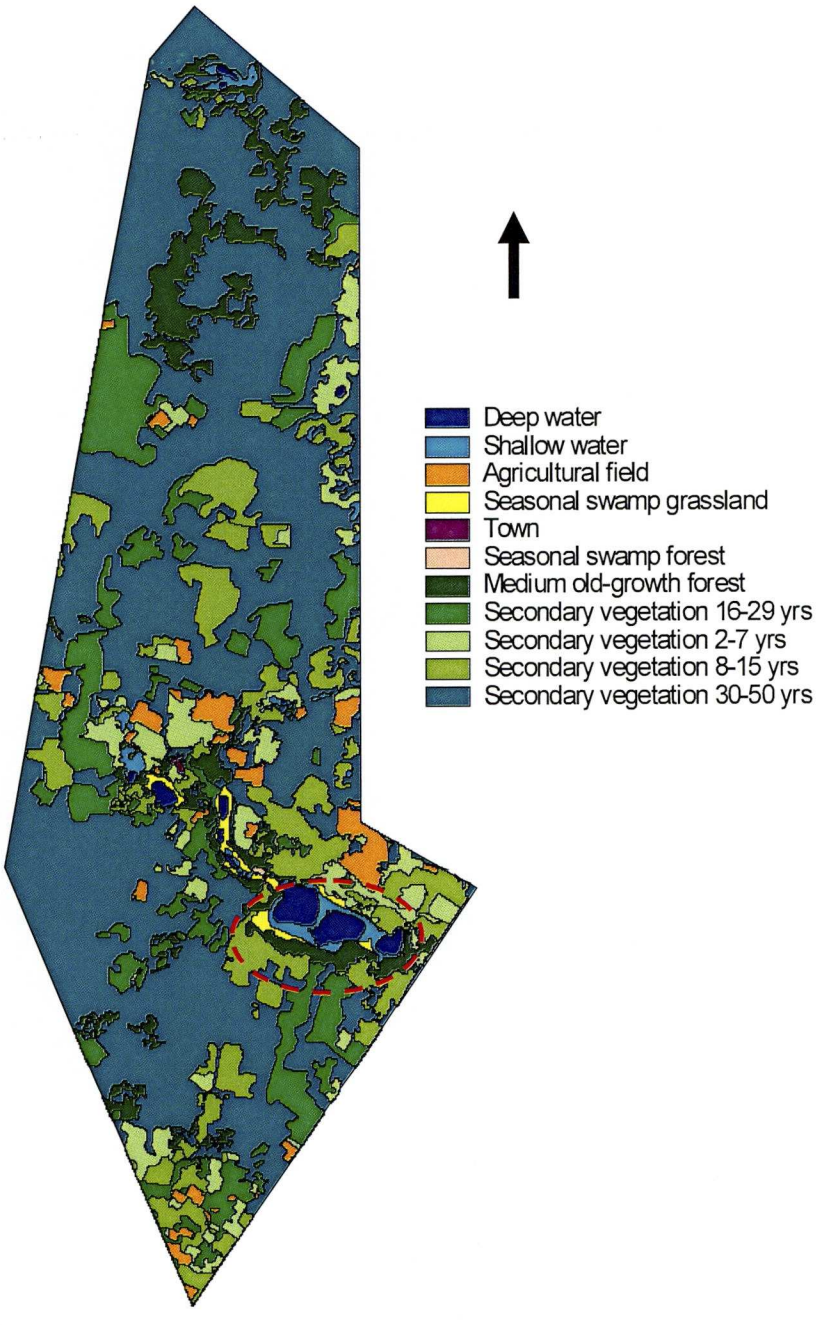

Figure 2.1 *Otoch Ma'ax Yetel Kooh* protected area in the state of Yucatan, Mexico which indicates the different forest types. The circled area represents the area in the protected area where the two communities of spider monkeys range (adapted from Ramos-Fernandez, Vick, Aureli, Schaffner & Taub, 2003).

Two primate species inhabit the forest, spider monkeys (*Ateles geoffroyi yucatanenesis*) and howler monkeys (*Alouatta pigra*). Spider monkeys were found in both medium and, with lower density, also in successional forest (Ramos-Fernández & Ayala-Orozco, 2003). Two of their main feeding tree species (*Metopium brownei* and *Guazuma ulmifolia*) are more abundant in successional than medium forest (Ramos-Fernández & Ayala-Orozco, 2003). Most of the medium forest is distributed along the south-western and south-eastern side of the main lagoon, which represents the area of spider monkeys' major use (see area indicated in Figure 2.1).

It is worth mentioning that the management of the protected area has turned into a successful case of sustainable development. The villagers of Punta Laguna were the ones to instigate the interest in making the area around Punta Laguna a natural reserve. Since 1990, the area was the subject of interest and study by scientists from several institutions. The Mexican NGO, Pronatura, mitigated internal conflicts that arose in the community. After the declaration as NPA, the Governmental Commission for Natural Protected areas (CONANP) provided support for the creation of several sustainable projects, including a low impact eco tourism industry in which villagers take tourists through the forest in part to look at and follow spider monkeys. A key element in gaining NPA status for the region was the scientific information collected on site on various ecological aspects of the reserve. The NPA *Otoch Ma'ax Yetel Kooh* is a unique example of natural and cultural conservation, which continues offering valuable scientific information. However, the conversion of the study area into a NPA has meant that the Eastern community was frequently exposed to tourists. Therefore, it is possible that the presence of visitors impacts the natural behaviour of spider monkeys in the Eastern community.

2.2 Study species

Among the New World Atelines, the genus *Ateles* is described as the "ripe-fruit driven, upper canopy suspensory brachiator" (Rosenberg, Halenar, Cooke & Harwig, 2008, p. 20). Spider monkeys' geographical distribution ranges across a wide area of the Neotropics; longitudinally, from the most northern state of Veracruz, Mexico, to northern Bolivia and, in latitude, from the pacific coast of Ecuador to regions of north-eastern to South America in Suriname and Guyana (Rowe, 1996). The genus

Ateles is the least dimorphic among the atelines with *A. geoffroyi* males weighting an average of 8.2 kg and females weighting an average of 7.5 kg (Fords & Davis, 1992). The taxonomic studies of *Ateles*, initially based on cranial morphology and pelage variations, yielded four distinct species (*A. belzebuth, A. paniscus, A. fusciceps and A. geoffroyi*) (Kellog & Goldman, 1944, cited in Collins, 2008). Subsequent studies on molecular, morphological and chromosomal variation produced slightly varying taxonomic proposals. There is generally wide agreement about the classification of the species (Groves, 1989; Froehlich, Supriantna & Froehlich, 1990; Collins & Dubach 2000; Nieves, Ascunce, Rahn & Mudry, 2005; Collins, 2008). However, recently *A. fusciceps* has been classified as a subspecies of *A. geoffroyi* (Rylands, Schneider, Mittermeier, Groves & Rodriguez-Luna, 2000; Collins, 2008). There is also some ambiguity in respect of the number of sub-species belonging to each species. Ten subspecies of *A. geoffroyi* have been proposed by Collins and Dubach (2000), of which two (*A. g. vellerosus* and *A. g. yucatanensis*) are found in Mexico in medium high perennial forest and lowland perennial forest (Estrada & Coates-Estrada, 1988).

The average ranging patterns of spider monkeys lies between 150 and 350 hectares, where upper levels of the canopy are preferred to lower strata. Habitat use is strictly related to seasonal variations that reflect the resource distribution and availability. In fact, more than 50-90% of spider monkeys' diet is represented by ripe fruits, which are highly nutrient rich and are dispersed patchily in the canopies of the trees (van Roosmalen & Klein, 1988; Di Fiore, Link & Dew, 2008). The diet of spider monkeys is highly selective with a low number of species, but other species are used in an opportunistic way (González-Zamora, Arroyo-Rodríguez, Chaves, Sánchez-López, Stoner, et al., 2009). The fruits of *Ficus* spp. and *Brosimum* spp. are consumed in particularly high amounts (Gonzalez-Zamora, et al., 2009). The secondary dietary component of spider monkeys' diet is leaves, whose consumption may increase when there is a shortage in higher quality foods (Gonzalez-Zamora, et al., 2009). Flowers, insects, bark, minerals, fungi and pseudobuds constitute a much smaller portion of the dietary intake (van Roosmalen & Klein, 1988; Di Fiore et al., 2008).

Spider monkeys live in multi-male multi female societies characterised by a high degree of fission –fusion dynamics (FF dynamics, Aureli et al., 2008). This characteristic of societies means that community members are rarely all together and continuously associate in subgroups that vary in size and composition (Symington, 1990). This very flexible social structure is related to the ecological constraints of spider monkeys' habitat. Subgroup size can be adjusted to the uneven distribution of food resources, avoiding a high degree of intra-group competition in this highly frugivorous species (Chapman, 1990; Symington, 1990; Shimooka, 2003; Lehman, Korstjens & Dunbar, 2007; Wallace, 2008). Although community members occasionally join in big mixed-sex subgroups during resting or playing periods, subgroups are often sexually segregated. Males associate in relatively stable subgroups, whereas females' foraging subgroup size depends on the food abundance and the presence of infants (Fedigan & Baxter, 1984; Chapman, 1990; Shimooka, 2003, 2005). Most spider monkey females disperse when they reach sexual maturity, whereas males are philopatric (Symington, 1988; Vick, 2008). A long prehensile tail and particularly long forelimbs are adaptive traits to an arboreal life (Rosenberger et al., 2008) as spider monkeys are highly specialised for brachiation and below-branch suspended locomotion. Females are easily discernible by the presence of a hypertrophied elongated clitoris.

2.3 Study Population

The two communities of spider monkeys I investigated inhabit the natural reserve Otoch Ma'ax Yetel Kooh. One community ranges in the south-western side of the main lagoon, whereas the other community ranges in the south-eastern side of the lagoon. The two groups of spider monkeys have been studied continuously since January 1997. Spider monkeys were therefore already well habituated to the presence of observers and were all individually identified. During the study period, from January 2005 to September 2006, at least four infants were born into the two communities, two in the Western community and two in the Eastern community. One adult male (Licho) was not seen again after the occurrence of hurricane Emily in July 2005. At the beginning of the data collection the Eastern community included 23 individuals, whereas in the Western community at least 40 individuals were present (sex and age composition are reported in Table 2.1). Relatively short appearance of new individuals in the Western group together with the temporarily absence of other

individuals, created a certain level of ambiguity in respect of the number of spider monkeys in that group. The age classes were determined in the following way, individuals were classified as infants from the time they were born until the mother gave birth to her next infant following Vick (2008), which typically occurred when individuals were three years of age. After this stage individuals were considered juveniles up until the age of five, which is when juvenile males associated frequently with male adult subgroups and corresponds to the year during which females are most likely to emigrate from their natal territory (Vick, 2008). All the other individuals were considered adults, including the newly immigrated females.

Table 2.1 Age and sex composition of the two communities of spider monkeys in Otoch Ma'ax Yetel Kooh.

	Adult males	Adult females	Juvenile males	Juvenile females	Female infants	Male infants
Eastern community	4/3	8	3	2	2	5
Western community	7	16	6	9	2	2

2.4 Materials

Data were recorded with the use of digital recorders (Olympus digital hand-held recorder) and subsequently transcribed to Excel files in the computer. Observation quality was improved thorough the use of 10X42 Olympus binoculars and a Fastime stopwatch with repeat countdown timer was also employed.

2.5 Data collection

Data were collected at the field site in 2005 and 2006 in two nine month blocks from January to September each year. Observations were taken five days a week alternatively during the morning and afternoons. For observations during the first half of the day, individuals were found at their sleeping trees at dawn and followed as long as possible up to six hours. Observation sessions that commenced at 1200 hrs involved either searching the core area until a subgroup was encountered or by relayed information on subgroup locations from other researchers. The first subgroup encountered would be followed and when fission occurred, the subgroup with individuals with the least number of focal observations was chosen to continue the subgroup follow. The monkeys would be followed to their sleeping trees, in order to

facilitate their location on the following morning. When monkeys were lost, the observers would search for another subgroup that would then be followed with the same rules. Individuals were considered part of the same subgroup when they were less than 30 m away from any other individual of the same subgroup in a chain rule method (see Slater, Schaffner & Aureli, 2007). Subgroup composition was scored every 20 minutes and individuals were deemed to have fissioned from the group if they were not seen in two consecutive scans. This was an extremely reliable estimate as when individuals are scored as fissioned in this manner there is only a 5% chance they will return to the subgroup in the same observation day (Aureli & Schaffner, unpublished data). Fusions were deemed to occur when two different subgroups comprised of different spider monkeys from the same community joined together and this was scored on an all occurrences basis. Fifteen minute focal animal samples (Martin & Bateson, 1993), with 30 seconds instantaneous sampling intervals (Martin & Bateson, 1993), were taken on all adult and juvenile individuals in each community. Behaviours that were scored using instantaneous sampling during focal observations are presented in Table 2.2 and behaviours scored using continuous observations are presented in Table 2.3. The behavioural ethogram was adopted from previous ethograms used on this same population of spider monkeys (Aureli et al., 2006; Slater, et al., 2007), which in turn were developed from pilot observations and earlier published ethograms of spider monkey behaviour (e.g., van Roosemalen & Klein, 1988). Repeated focal animal sampling on the same individual were conducted at least one hour after the previous observation. Focal observations were conducted giving priority to those individuals for whom not many focal observations were available in the attempt to reach the most uniform number of observation on any individual. Fission and fusion events and aggressive interactions were taken on an all occurrences basis (Martin & Bateson, 1993). Four field assistants provided support in finding, following and identifying the monkeys. Field assistants also participated in the collection of aggressive behaviour, fission and fusion events, particularly during focal observations when the observer was unable to monitor other events in the subgroup. Every focal animal sample included information about the overall subgroup activity, the location of the subgroup in the forest, and the composition of the subgroup at the time the focal commenced.

Table 2.2 Ethogram of behaviours recorded in instantaneous scan samples during the focal observations.

Solitary Behaviour	Definition
Feed/ Forage	Focal consumes food or actively searches for food items by smelling, touching or directing their gaze toward food items
Drinking	Focal consumes water from tree holes or directly from the lake
Rest	Focal sits or lies down without scanning the environment
Deep rest	Focal is sitting or lying down with closed eyes or with head hidden into own or another monkey's body and is not scanning the environment.
Moving	Focal individuals locomotes from one position to another by either walking on substrates, sliding on substrates, brachiating, leaping or bending trees with their body weight to move to another tree
Dangling	Focal hangs from limbs and/or tail without feeding or scanning the environment
Scanning	Focal is behaving in a vigilant manner by moving the head from right to left repeatedly.
Self-touching	Focal grooms itself, self –scratching (see Table 2.3 for separate definition of scratching) or uses fingers or toes to contact other parts of its body
Social Behaviour	
Proximity	Focal is in proximity within arm's reach of another monkey , (but not in contact)
Passive contact	Focal is in physical contact with other individual (sitting in contact or huddling, arm can be wrapped around others as in wrapping huddle)
Wound cleaning	Focal licks or touches a wound of its own or another individual
Grappling	Focal involved in sequence of behaviours including more than one of the following elements: embraces, tail wrapping, face greeting, face touches, genital contact with prolonged eye contact
Copulation	Female sits on male's lap and male responds by wrapping his legs around the female's thighs, intromission may last 10-30 minutes
Aggression/attack	Focal involved in interaction that includes one or more of the following elements: chasing, lunging, grabbing, biting, or facial threats.
Play	Focal involved in chasing, wrestling, slapping, or mock bite in a non-aggressive manner usually accompanied by vocalization
Other social	Focal involved in social behaviour other than the above
Other non-social	Focal involved in non social activities other than the above
Out of view	Focal is out of view at scan time

Table 2.3 Ethogram of behaviours recorded for all occurrences during focal observations in which the focal animal could be the actor or the recipient of the behaviours.

Social Behaviour	Definition
Approach	One individual moves toward another to at least arm's reach
Leave	One individual moves away from another to a distance greater than arm's reach
Solicit Grooming	One individual presents body part to another individual
Pass by	One individual moves toward another individual to a distance of less than arm's research but continues to move past the individual without stopping
Allo-grooming	One individual manipulates the fur of another individual with its hands or its mouth
Wound cleaning	One individual licks or touches a wound of its own or another individual
Aggression-short chase without physical contact	One individual rapidly follows a retreating individual without making physical contact and the retreating individual emits distress vocalisations, the pursuit is ceased after the initial retreat
Aggression – long chase without physical contact	One individual rapidly follows a retreating individual without making physical contact and the retreating individual emits distress vocalisations and is forced to move down to the lower part of the canopy often to the ground, before the pursuit is ceased
Aggression with physical contact	Actor approaches victim and bites, strikes or grabs part of the victim's body. It can be brief in which the victim is immediately released from the actor or prolonged in which the actor repeatedly bites, strikes and/ or grabs part of the victim's body multiple times and the victim may counter the aggression with both parties in contact for a prolonged period of time.
Support victim	One individual intervenes in an aggression by coming between the actor of the aggressor and victim
Support actor	One individual joins in the aggression with the actor and attacks the victim
Embrace	One individual wraps one arm or both arms around another's shoulder, head or waist
Pectoral sniff	Monkey places its nose at the chest or arm pit region of another
Kiss	Two individuals put their faces in close proximity in a cheek-to-cheek position, usually with no contact or only minor contact of the cheeks between the two individuals.
Face greeting	One individual gazes in direction of other and purses lips outward in a wide kiss-like gesture
Genital sniff	One individual places its face and nose in the anogenital region of another individual
Body sniff	One individual places its face and nose in a body region of another individual other than genitals and chest/armpit
Genital touch	One individual uses its fingers to make contact with the genitals of another individual.

Table 2.3 continued

Solicit copulation	One individual invites other to copulate (copulation may or may not follow)
Displacement	One individual causes another individual to move from its location by approaching without aggression
Bridging	One individual, normally a mother, positions her body across a gap in the canopy and holds the position while a juvenile approaches. If the juvenile uses the body to cross the gap it was scored as 'bridge used; if the juvenile forgoes the bridge it was scored as 'bridge not used'
Solitary Behaviours	
Self-scratching	Repeated rhythmic scraping of fingers on individual's own fur or body, a new scratching event was scored whenever there was at least a five second interval from when one scratching event ended and the next one started
Branch sniff/lick	Focal touches nose or tongue to substrate
Genital rub	Focal sits and moves genitals back and forth along a branch
Genital drag	Focal moves in a sitting position and drags genitals along branch
Chest rub	Focal moves chest back and forth against substrate
Mouth rub	Focal moves mouth back and forth against substrate
Branch shake	Focal shakes branch to other monkey or observer
Threat	Focal makes a face by opening mouth and exposing teeth, moving the head forward rapidily
Leaf Chest rubbing	Focal rubs leaves on pectoral area predominantly, but may include other parts of the body
Mouth to Chest leaf rubbing	Focal does as in leaf chest rubbing but also chews leaves and rubs them on the mouth and then the chest and back to the mouth repeatedly
Out of view Starts	Scored whenever a focal animal was not visible to the observer
Out of view Ends	Scored when a focal animal was again visible to the observer.

Data collection was designed with the aim of studying the mechanisms that regulate spider monkey conflict and aggression. Therefore, I recorded several different types of focal animal samples. I collected baseline focal animal samples when no special events of interest were taking place. However, whenever a fusion event occurred, I collected a post-fusion focal observation on one individual. Immediately following an aggressive interaction, I collected a post aggression focal observation (PC) on one of the combatants involved in the conflict. Finally, in the immediate aftermath of an approach in which an embrace or pectoral sniff or kiss took place I collected a post-embrace focal observation on one of the individuals

involved in the embrace. The number of focal observations for each category is presented in Table 2.4 per year. Additional detail regarding the different focal samples is provided in Chapters 4 and 5.

Table 2.4 The number and year of different types of focal observations used in my thesis.

Type of focal observation	2003	2004	2005	2006
Baseline focals	-	-	571	441
Post-fusion	-	-	70	17
PC	11	18	32	5
Post-embrace	-	-	42	7

During 2006, the last four months of data collection, from June through September were carried out by two extremely experienced field assistants Nicola Forshaw (NF) and Norberto Asensio (NA) who had both worked previously on the larger spider monkey project managed by my supervisors. Both individuals underwent training on my protocol and inter-observer reliability checks were performed between me and NF and NF and NA. Inter-observer reliability checks were tested with proportions of agreement between the two sets of scores.

Chapter 3

Components of social relationships

3.1. Quality of relationships in non-human primates

Most diurnal non-human primates live in groups (Kappeler, 1999). Their social organisation results from an optimisation process that maximises benefits and minimises costs of group living (Lehman, et al., 2007). Therefore, sociality can be considered an adaptive trait selected by evolutionary processes (Wrangham, 1987). Group-living species are characterised by the permanent association of at least three adult individuals of mixed sex composition with varying degrees of spatial and time associations (Kappeler, 1999). Group-living animals gain benefits from the presence of other conspecifics in many ways, including detection and protection from predators, finding food, facilitated access to ecological, social and reproductive resources, and provision of infant care (van Schaik, 1983; Pulliman & Caracao, 1984; Clark & Mangel, 1986). Cooperation is therefore extremely important for the survival of group members. Living in close proximity to members of the same species entails direct costs as there is increased competition for food resources and mates (Watts, 1985), as well as indirect costs from conflicts of interest that arise about decisions at a group level, such as where to go and what to do (van Schaik & Noordwijk, 1986). Nevertheless, the advantages of cooperation outweigh the costs entailed in group-living species.

The coexistence of individuals in a social group implies repeated and frequent encounters between group members. These conditions lay the ground for the development of social relationships (van Schaik & Aureli, 2000). Hinde (1976) proposed a conceptual framework to describe social structure in non-human primates. It involved three levels: social interactions, social relationships and social structure. Interactions are defined by content and quality and may differ according to the relationship that the participants have with each other. Relationships between two individuals are shaped by the temporal patterning of content and quality. It implies a series of interactions between two individuals over time. Thus, a relationship is a dynamic concept that is influenced by the past interactions between individuals. The social structure is defined by the patterns of relationships existing between group members that occur over a period of time. Adopting a more functional approach,

Kummer (1978) emphasised the adaptive aspect of a social relationship. The way an individual 'A' interacts with its partner 'B' can influence B's behaviour toward A and thus A's chances of survival or reproductive success. In this respect a relationship is an investment in which social interactions are used to influence the partner's behaviour to its own advantage. Thus, individuals can increase or decrease their social partner's success (Kummer, 1978).

3.1.1 Identifying the components of social relationships

Social relationships can also be characterised by different qualities. For example, three components of social relationships have been suggested: value, security and compatibility (Cords & Aureli, 2000). The value of a relationship expresses how "useful", in terms of reproductive success, one partner is to the other. The value of a relationship is interpreted in terms of inclusive fitness benefits that a subject gains from interacting with another group member (Kummer, 1978; Cords, 1997; Wittig & Boesch, 2005). The degree to which one individual can be valuable to another depends, however, on its behavioural tendencies (Kummer, 1978). An individual's availability (how accessible he or she is), its quality (social status, reproductive condition, knowledge, skills) and how willing it is to contribute positively to the relationship constitute the value it has for prospective partners (Aureli & Cords, 2000). Security is the predictability of the partner's response to social interaction. The more consistent the partner's responses are over time the easier it is to predict them (Cords, 1988; Cords & Aureli, 2000). The level of compatibility is given by the historical pattern of interactions within a relationship that determines the degree of tolerance between partners.

Despite the attempt to categorise and define relationship quality in primates, a clear picture is still lacking. The inclusive fitness benefits underlying social behaviour among kin have been used to explain patterns of affiliation and cooperation among a wide variety of animals (Maynard-Smith, 1964; Trivers & Hare, 1976; Gouzoules & Gouzoules, 1987; Parker, Waite & Dereck, 1995), as well as the value of a relationship (de Waal, 1989; Kappeler & van Schaik, 1992; Cords & Thurnheer, 1993; Aureli 1997). Most of the studies conducted so far on relationship value have examined its influence on post-conflict behaviours, especially reconciliation (Kutsukake & Castles, 2001; Cooper, Bernstein & Hemelrijk, 2005;

Wittig & Boesch, 2005). The valuable relationship hypothesis states that agonistic encounters are more likely to be followed by reconciliation when the two opponents share a valuable relationship (Cords & Aureli, 2000). Indeed, kin are more inclined to reconcile compared to non-kin (Cords, 1988; Aureli, et al., 1989; Aureli & van Schaik, 1991; Judge, 1991; Aureli, et al., 1997). However, genetic relatedness is not a necessary prerequisite for a valuable bond. For example, in wild chimpanzees (*Pan troglodytes*) social partners are not chosen on the basis of genetic ties (Mitani, Merriwether & Zhang, 2000). Under high density conditions rhesus monkeys (*Macaca mulatta*) opt for a strategic partner choice that is not kin driven (Call, Judge & de Waal, 1996). In addition, kinship did not influence reconciliation in several species of primates whose social systems are less kin biased (Cords, 1988; Cords & Aureli, 1993; Aureli, et al., 1997; Arnold & Aureli, 2007).

The value of a relationship between two individuals has been frequently associated with particular sex combinations that are more likely to affiliate or form alliances than others, such as male-male dyads in chimpanzees (Mitani, et al., 2000; Watts, 2006; Koski, et al., 2007) and male-female dyads in gorillas (*Gorilla gorilla*, Watts 1995; Cordoni, Palagi & Borgognini Tarli, 2006).The extent to which individuals support each other during aggressive interactions is also considered a means to evaluate valuable relationships (Cords, 1997; Cooper, et al., 2005; Patzelt, Pirow & Fischer, 2009). Conversely, "compatibility" usually coincides with "friendliness". Dyads of individuals that engage in a high level of affiliation are said to be friendly (Cords, 1997). As a result, grooming rates are mostly employed to measure levels of compatibility because it implies a high degree of social tolerance (Cooper, et al., 2005; Koski et al., 2007a). Furthermore, grooming has been used to measure value because of the beneficial effects it can provide to the recipient (cf., Boccia, Reite & Laudenslager, 1989; Aureli, Preston & de Waal, 1999; Aureli, et al., 2002). Relationship security has been measured using the degree of equality in grooming reciprocation (Fraser, Schino, Aureli, 2008; Majolo, Ventura & Koyama, 2009) and as a degree of variation in proximity and grooming within two individuals over time (Fraser, et al., 2008). Rates of negative outcomes to approaches have also been suggested as a means to assess security of relationships (Cooper, et al., 2005).

Since the distinction of relationship quality in three components is relatively recent, most of the primatology literature refers to the general term " relationship quality" in its broad meaning: grooming (Aureli, et al.,1989; Palagi, Paoli & Borgognini Tarli, 2004; 2005; Schino, Rosati, Geminiani & Aureli, 2007); contact sitting (Palagi, et al., 2004; 2005); agonistic support (Smuts, 1985; Walters & Seyfarth, 1987; Aureli, et al.,1989); aggressive tendency (Schino, Rosati, Geminiani & Aureli, 2007) and cooperation (Aureli, et al. 1989; Koski, et al., 2007). Consequently, ambiguity remains about which behaviours characterise which components of relationship quality. In addition, the assessment of relationship quality through the selection of specific behaviours might be reductive and misleading. The measure of the components of relationship quality should take into account the role each behaviour plays in a given dyadic relationship and should not be influenced by the observers' perspective (Silk, 2002).

Principal components analysis (PCA) was employed to study mother-infant behaviour in Japanese macaques (Simpson & Howe, 1980, Tanaka, 1980; Schino, D'Amato & Troisi, 1995), vervet monkeys (Fairbanks & McGuire, 1987) and to investigate mating patterns and consortships in rhesus and Japanese macaques (Manson, 1997; Soltis, 1999). More recently, Fraser, et al. (2008) used the PCA method in a study of a captive group of chimpanzees. They identified three components of relationship quality in captive chimpanzees derived from nine behavioural measures that mapped onto the components of security, value and compatibility proposed by Cords and Aureli (2000). This method was successfully extended to the study of social relationships in ravens (*Corvus corax*) (Fraser & Bugnyar, 2010).

3.1.2 Social relationships in spider monkeys

Although there has been recent attention regarding the nature of spider monkey social relationships (see below), no study to date has investigated what components characterise the social relationships of spider monkeys. Social organisation plays a crucial role in defining spider monkeys' social relationships. Spider monkeys live in communities with a high degree of fission-fusion dynamics (Symington, 1990; Aureli & Schaffner, 2008). Individuals frequently split and merge into fluid subgroups creating opportunities to avoid or interact with other community

members. Subgroups are typically sex-segregated: adult males band together and travel long distances, whereas females spend more time with other females or alone, depending on the presence of infants and on the availability of food resources (Chapman, 1990). Sexually mature females disperse from the natal group, whereas males are philopatric (Symington, 1987; Shimooka, Campbell, Di Fiore, Felton, Izawa, et al., 2008). Due to these socio-ecological factors, adult females are not expected to share highly valuable relationships (Aureli & Schaffner, 2008), and the frequency of affiliative behaviours, such as grooming and embraces between females is indeed lower compared to that between males (Fedigan & Baxter, 1984; Ahumada, 1992; Slater et al., 2009). Affiliative interactions between females, especially embraces, are reported to increase in the presence of young infants possibly to communicate benign intent and reduce uncertainty (Slater, et al., 2007). Agonistic interactions usually involve recently immigrated females who are targeted by long-term resident females (Asensio, Korstjens, Schaffner & Aureli, 2008).

Male philopatry creates opportunities to build stronger relationships for male-male dyads (Di Fiore & Campbell, 2007). Relationships are tightly bound among males by their joint efforts to cooperate in intergroup encounters and patrolling boundaries to defend access to females and food sources from neighbouring communities (Shimooka, 2003; Wallace, 2001; Symington, 1990; Aureli et al., 2006). Therefore, highly valuable relationships are expected between males. Grooming and embraces are exchanged more often between males compared to other sex dyads (Ahumada, 1992; van Roosmalen & Klein, 1988; Slater et al., 2009). However, male-male relationships may vary across developmental stages. There is evidence that relationships between young males (juveniles and sub-adult) and adult males are characterised by uncertainty and potential high risk (Vick, 2008). Lethal aggression has been reported between males of the same community (Valero, Schaffner, Vick, Aureli & Ramos-Fernandez, 2006; Campbell, 2006). Furthermore, only adult-juvenile male associations appear to be involved in extremely long and intense grappling sessions (Klein, 1971). Such grappling sessions seem to be loaded with strong attraction as well as high uncertainty, which appear to reflect tension between the partners (Aureli & Schaffner, 2008). Grooming levels are reported to be lower in mixed sex and female-female dyads than male-male dyads, although some variability exists among differences in grooming frequency between female-male and

female-female dyads in different populations (Di Fiore & Campbell, 2007; Aureli & Schaffner, 2008).

Female-male relationships are characterised by a relatively high degree of agonistic interactions compared to other sex dyads (Fedigan & Baxter, 1984). However, the common female-directed male aggression is likely a form of ritualised sexual display and occurs more frequently when females are capable of conceiving young (Slater, Schaffner & Aureli, 2008). The female reproductive state is likely a key factor that influences male-female relationships over time.

A strong relationship exists between mothers and their offspring who are carried on their mothers' backs until their second year and are weaned between their second and third year of life (Vick, 2008). Mother – offspring relationships are characterised by high levels of affiliative interactions (Carpenter, 1935; Ahumada, 1992). In addition, mothers protect their juvenile and adult offspring, and juvenile and adult males and females are known to defend their mother under attack (cf., Aureli et al., 2006; Valero et al., 2006; Vick, 2008). Not much information is available regarding the influence of group tenure on relationships. There is however evidence that newly immigrated females are targets of aggression from other females, whereas long-term resident females receive almost no aggression (Asensio, et al., 2008). In addition, captive female spider monkeys in a well-established group exchanged embraces more often than females in a newly formed group (Pastor-Nieto, 2001) further suggesting that tenure may affect the social relationships at least among female spider monkeys.

3.1.3 Aims of the study

My first aim of the present chapter was to identify components of relationship quality using PCA to better understand spider monkeys' social relationships. The second aim was to investigate whether characteristics of the dyads, such as age combination, sex combination, kinship and relationship tenure had an effect on the components obtained. The results are interpreted in light of the current understanding of spider monkeys' social relationships and provide an original contribution to understanding the quality of social relationships in primates.

3.2 Methods

3.2.1 Subjects

The study subjects were 54 spider monkeys from two neighbouring communities: the Eastern and the Western communities, located in the protected area of *Otoch Ma'ax Yetel Kooh* (described in Chapter 2). Data were collected for all the monkeys who were individually recognised, excluding individuals under the age of three years.

3.2.2 Data collection

Data were collected using focal animal samples from 54 subjects, which involved scoring all occurrences and instantaneous scan samples of behaviours as described in Chapter 2. The following data were used for the analyses in this chapter: scans of proximity, contact, and grooming, and all occurrences of embraces, kisses, pectoral sniffs, grooming solicitation and aggressive behaviours. In addition, I noted all changes in subgroup composition on a continuous basis.

3.2.3 Data analysis

Eight measures were calculated for each of the 823 dyads and subjected to principal component analysis (PCA) to determine what factors characterised the social relationships among the studied spider monkeys (Table 3.1). PCA is a statistical technique that identifies which variables in a set of variables are correlated with one another. The correlated variables are then combined into components, which reflect underlying correlations among the variables (Tabachnik & Fidell, 2007). A considerable advantage of using PCA is to reduce numerous variables to a few components. The analysis starts out with a large number of variables, in my case eight different behaviours, from which components are derived. Then, the scores of the variables load high or low on the different components that are interpretable as factors (Tabachnik & Fidell, 2007). The naming of factors depends on the meaning of particular combination of observed variables that correlate highly with each factor (Tabachnik & Fidell, 2007).The first component accounts for the most variance within the sample, followed by other components that explain smaller portions of the variance and that are not correlated with the previous components. In the present study, a coefficient of correlation greater than 0.7 and lower than -0.7 were

considered high loadings. A varimax rotation was used to simplify the interpretation of the components (Tabachnick & Fidell, 2007). A minimum Eigenvalue of 1.0 was adopted to select the components extracted from the PCA analysis.

The following indices and scores are presented by dyad in matrices in the appendices that follow at the end the thesis.The *subgroup index* (Appendix A & I) between individual A and B was calculated using the total time A was in the same subgroup with B in A's focal samples and the total time B was in the same subgroup with A in B's focal samples divided by the sum of the total time of A's focal samples and the total time of B's focal samples. The *proximity score* (Appendix B & J) between individual A and B was obtained by dividing the sum of instantaneous scans A and B were in contact or proximity with each other by the sum of scans A and B were in the same subgroup. Similarly, the *grooming score* (Appendix C & K) was obtained by dividing the sum of scans in which A groomed B and B groomed A by the sum of total scans A and B were in the same subgroup. *Grooming symmetry* (Appendix D & L) was calculated by dividing the sum of scans A groomed B by the sum of scans A groomed B and B groomed A, where the smallest sum of grooming scans between A and B was used as the numerator. *Agonistic support* (Appendix E & M) was obtained by dividing the number of times A and B supported each other in agonistic conflicts by the number of opportunities A and B had to support each other. An opportunity was identified when individual A and B were in the same subgroup and one of them was involved in an aggressive interaction (excluding aggressive interactions between them). The *aggression rate* (Appendix F & O) was expressed by the number of aggressive interactions between A and B divided by the total time A and B were in the same subgroup. *Successful grooming solicitation* (Appendix G & N)was obtained by summing the number of successful grooming solicitations of A to B and of B to A and dividing the sum by the overall number of grooming solicitations from A to B and of B to A. A grooming solicitation was defined as successful when grooming was received within 30 seconds of solicitation (Chapter 2). The *embrace rate* (Appendix H & P) was determined by dividing the number of embraces between A and B by the total time A and B spent in the same subgroup.

Table 3.1. Variables used for PCA analysis.

Variable name	Definition
Subgroup index	Proportion of time spent in the same subgroup
Proximity	Proportions of scans spent in proximity and contact witheach other
Grooming	Proportion of scans the partners spent grooming each other
Grooming symmetry	Symmetry in grooming within the dyad
Support	Frequency of support / opportunity for support
Aggression	Rate of aggressive interactions within the dyad
Successful grooming solicitation	Proportion of grooming solicitation that were successful within the dyad
Embrace	Rate of embraces within the dyad

All variable were calculated for each of the 823 dyads of study subjects.

3.2.3.1 Variables characterising social relationships

The effect of four characteristics of social relationships on the components extracted with PCA was assessed using linear mixed models (LMMs). LMMs are a statistical modelling approach that go beyond conventional general linear model techniques (e.g., analysis of variance) and circumvent some of the limitations of statistical approaches by allowing for data that are not independent. Furthermore, they avoid the problems of pseudo-replication, and in some cases negate the need for a normal distribution and handle missing cells of data (McCollogh & Searle, 2001; Garson, 2008). Fixed variables serve as the independent variables in the model and variables, such as dyad or actor identity, are entered into the model as random factors to control for the repeated samples from the same individual. Thus, LMMs use all available data, which potentially increases the power of the test.

In the present study, each dyad of the study subjects was categorised by the following characteristics: sex combination, age combination, kinship and relationship tenure, which served as the independent variables. Sex combinations included male-male, female-male and female-female dyads. Individuals were classified as either adult or juvenile (Chapter 2), and age combinations were therefore adult-adult, adult-juvenile and juvenile-juvenile. Individuals were considered as kin only when maternal relatedness was known ($r \geq 0.25$). All other dyads were considered as non kin. Relationship tenure was defined as the length of time individuals were together

in the community. Dyads with at least one individual born or immigrated into the community from the start of 2003 were considered to have short-tenure relationships, whereas dyads in which both individuals were in the community before 2003 were considered to have long-tenure relationships. Dyads were also classified according to the community to which they belonged, Eastern or Western, and this variable was entered as a random factor. To control for between-subject variation and non-independence of data points, partner identities were included as additional independent variables in all the analyses. The dependent variables were the scores for each dyad from the components that were extracted from the PCA. The best model was selected using Akaike's information criterion (Tabachnik & Fidell, 2007) and a significance level 0.05 was adopted. All statistical tests were conducted with SPSS v. 16.

3.3 Results

3.3.1 Components of relationship quality

The results from the PCA revealed that from the eight variables only five variables were loading strongly on the components. I removed 'grooming symmetry', 'agonistic support' and 'successful grooming solicitation' because their scores were available for only a subset of dyads and their loadings were low on any component. Without these three variables the remaining five variables loaded more clearly onto the components. Each variable loaded highly only on one of the two components. The variables and the loadings are presented in Table 3.2. Two components were extracted by the PCA explaining 63.9% of the total variance. Component 1 accounted for 37.8% of overall variance and had high positive loadings for subgrouping index, proximity and grooming, indicating that the component reflected tolerance and affiliation and was therefore termed Compatibility. Component 2 accounted for 26% of the total variance and was characterised by high positive loadings of Aggression and Embrace. Given that component 2 consisted of behaviours that suggest uncertainty, I labelled it Risk. The term Risk seemed to be more appropriate than Security. The high load of aggression on component 2 suggests that apart from uncertainty there was a degree of risk to the partners captured in the component. Some risk is also entailed in embraces. During embraces

individuals expose parts of their body (throat and shoulders) to the recipient's mouth, thus running the potential risk of serious injury (cf., Aureli & Schaffner, 2008).

Table 3.2. Varimax rotated component matrix.

Variables	Components	
	1	2
Subgrouping index	0.785	-0.065
Proximity	0.801	0.004
Aggression	-0.098	0.797
Embrace	0.036	0.814
Grooming	0.789	-0.029

Values represent coefficients of correlation between each variable and each component. Values above 0.7 and below -0.7 were considered high loadings.

3.3.2 Effects of relationship characteristics on relationship components

Then, I applied an LMM to investigate the effects of relationship characteristics, as independent variables, on the two components from the PCA (Table 3.3). Three of the four independent variables had an effect on the components of relationship quality. Age combination had no significant effect on the two components. Kinship had a significant positive effect on Compatibility, suggesting that related individuals were more compatible than non-kin (Table 3.4). Sex combination of the dyad also affected Compatibility (Table 3.4). Male-male dyads were more compatible than female-male and female-female dyads, whereas female-female and male-female dyads did not differ in their compatibility. Relationship tenure had no effect on Compatibility, meaning that individuals who had spent more time together in the community were not more likely to be compatible. Risk was not significantly affected by kinship, although sex combination did affect the degree of Risk. Male-male dyads had more risky relationships than female-male and female-female dyads. Relationship tenure also had an effect on Risk. Individuals with longer tenure together in the community had more risky relationships.

Table 3.3 Predictors used for LMM on the effects of relationship characteristics on components of relationship quality.

Fixed factor	Combination of sex and age, kinship, tenure and partner identities
Random factor	Actor identity
Dependent factor	Scores of compatibility and risk extracted from PCA

Table 3.4 Independent variables in the best LMM indicating the influence of relationship characteristics on the two components of relationship quality.

Dependent variables	Independent variables	β	SE	t value	p value	95% confidence intervals
Compatibility	Kinship	2.47	.18	13.99	< 0.001	2.13 - 2.82
	FF-FM	.03	.09	-.37	0.71	-.14 - .22
	MM-FM	.61	.14	4.46	< 0.001	-.89 - .34
	FF-MM	-.58	.14	-4.13	< 0.001	-.86 - -.30
Risk	FF-FM	-.06	.12	-.51	.61	-.31- .18
	MM-FM	.59	.18	3.31	< 0.001	.24 - .94
	FF-MM	-.79	.24	-3.285	< 0.001	-1.25- -3.15
	ST-LT	-.23	.13	-1.743	.084	-.0.48 - -0.03

MM=male–male dyads; MF=male–female dyads; FF=female–female dyads.
ST=short tenure; LT= long tenure.
Only variables present in the best model are shown.
To compare FF vs. MM data, the models were rerun, altering the order of the levels.

3.4 Discussion

The first aim of the chapter was to determine what components underlie the social relationships in wild spider monkeys. I used eight behavioural variables collected from two communities of spider monkeys to identify components of relationship quality through PCA. Three of the eight variables, grooming symmetry, agonistic support and successful grooming solicitation, were not used in the PCA because they did not contribute meaningful variance to the extracted components. Results for the remaining five variables were clear-cut, with each variable loading strongly only on one of the two extracted components. Subgrouping index, proximity score, and grooming score loaded strongly and positively on component 1, which I labelled Compatibility. Embrace and aggression rates loaded highly on component 2, which I labelled Risk. Thus, I was able to identify underlying components that characterise the social relationships in wild spider monkeys.

3.4.1 A lack of value in spider monkey relationships

In my study I did not find a component of relationship that reflected the Value of a relationship. The lack of a component that could reflect the Value of a relationship in this study is likely due to the absence of direct fitness benefits behaviours used as variables in the PCA. In Fraser et al.'s (2008) study on components of relationships in chimpanzees, agonistic support and begging were included in the PCA and these behaviours helped in identifying a component labelled

Value. In my study, the variable agonistic support was removed from the analysis of PCA because it did not contribute meaningful variance to the components and without it the remaining variables loaded more clearly onto the components. A larger dataset with more cases of agonistic support and other cooperative behaviours might result in a component of Value. The fact that I was unable to identify Value as a component in my study is not sufficient evidence to conclude that no spider monkey relationships are valuable. Given the alteration in the spider monkeys' behaviour during 11 of the 18 months of my period of data collection (see Chapter 6), the frequency of behaviour that reflected value was too low. Future studies on the same population or different populations would likely have sufficient frequencies of relevant behaviours to identify a component of Value.

3.4.2 Compatibility component of social relationships

The three variables that underlie the characteristic of Compatibility reflect varying degrees of affiliative and tolerant behaviours. In accordance with the definition proposed by Cords and Aureli (2000), Compatibility is characterised by the frequency and duration of affiliative interactions that reflect the general tenor of the relationship. Two of the three variables that define Compatibility, i.e. subgrouping index and proximity, are not usually associated with providing direct fitness benefits related to behavioural exchanges which are, instead, thought to express the "value" of a relationship (Cords & Aureli, 2000). Grooming is usually used in valuable relationships because it has been demonstrated to provide fitness benefits (Shutt, MacLarnon, Heistermann & Semple, 2007; Boccia, et al., 1989). However, grooming also can indicate a level of general tolerance in a relationship (Assamese macaques: Cooper, et al., 2005; e.g., chimpanzees: Koski, et al., 2007), and in my analysis loaded with other measures that also reflect high tolerance and not value (i.e., proximity and subgrouping index). Compatibility also includes subgrouping index, which can be viewed as a measure of association in societies with high fission-fusion dynamics. Thus, in my study Compatibility appears to capture the underlying functions of the three variables.

Other studies interpreted Compatibility by using degrees of tolerance to approaches in chimpanzees (Fraser, et al., 2008) and in ravens (Fraser & Bugnyar,

2010), or time spent in proximity without receiving aggression or being displaced in long-tailed macaques (Cords & Aureli, 1993). In my study I did not measure tolerance following approaches and it is certainly worth addressing in future studies on spider monkeys, although it is very likely that in my study the key measure of intolerance was provided by subgrouping index, in which individuals with high intolerance were unlikely to be in the same subgroup. This measure of subgrouping index, however, was not appropriate in studies of captive chimpanzees (Fraser, et al., 2008) or in captive long-tailed macaques (Cords & Aureli, 1993) as the captive settings did not allow for individuals to position themselves in different subgroups.

Compatibility was affected by the relationship characteristics of sex combination, and kinship. Kin were more compatible partners than non-kin. The effect of kinship on compatibility might be related to the high association in subgroups of mothers with their offspring (Fedigan & Baxter, 1984; Chapman, 1990). In fact, females and their offspring, who can be solitary or more gregarious depending on food availability and the presence of infants, typically range together and are rarely separated (Chapman, 1990; Symington, 1990; Shimooka, 2005). Furthermore, mothers and their offspring groomed each other often and showed high proportions of contact and proximity. Adult and juvenile females, which are likely to be mother –offspring, are reported to exchange high rates of grooming (Fedigan & Baxter, 1984; Ahumada, 1992; Mc Daniel, 1994, unpublished PhD; Vick, 2008). Thus, the high proportions of proximity and the rates of grooming between mother and offspring together with their subgrouping association, probably accounts for the kin effect on Compatibility.

Sex combination also had an effect on Compatibility. Male-male dyads were more compatible than male-female and female-female dyads. This result concurs in part with what is understood about the nature of male-male relationships in spider monkeys. Male-male relationships are reported as the strongest in spider monkeys because of the high rate of cooperative behaviour (Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988; Symington, 1990; Wallace, 2001; 2008; Shimooka, 2003; Aureli et al., 2006; Aureli & Schaffner, 2008). Adult males not only cooperate with each other, but they are also more affiliative with each other than adult females (Fedigan & Baxter, 1984; Ahumada, 1992; Slater et al., 2009). In particular,

grooming is more frequent between males compared to other sex combinations (Ahumada, 1992; van Roosmalen & Klein, 1988; Slater et al., 2009). In addition, males presented a high subgrouping index, as they associate typically in multi-male subgroups (Chapman, 1990; Symington, 1990; Shimooka, 2005). The subgrouping pattern also likely accounts for the high loading onto Compatibility of male-male dyads.

My findings in part contrast with the finding of a similar study conducted on chimpanzees (Fraser et al., 2008) where the highest compatibility was between females. Spider monkeys and chimpanzees share a similar social system, which in the wild is characterised by male philopatry, female emigration from the natal community and a high degree of fission-fusion dynamics (Symington, 1990), and therefore male-male relationships would be expected to be more compatible than other sex combinations. Fraser et al.'s (2008) study was conducted on captive chimpanzees, where female-female relationships might be altered compared to wild chimpanzees, particularly if many of the female-female dyads were composed of related individuals. In addition, many factors that may be important in shaping strong male bonds, such as defence from out-group males (Wrangham, 1999), the need to perform territorial boundary patrols (Watts & Mitani, 2001), and hunting and sharing meat (Mitani & Watts, 2001) are not present in a captive setting and in turn may obviate the need for highly compatible relationships between males.

3.4.3 Risk component of social relationships

On the second component extracted with PCA two variables loaded highly and positively: aggression and embrace rates. Previous research suggests that aggression is more likely to escalate between individuals for which the power asymmetry is low and the dominant-subordinate component of a social relationship needs to be reaffirmed (Preuschoft & van Schaik, 2000). In this way, aggressive interactions correspond to a degree of uncertainty with respect to ambiguous dominance relationships. Similarly, embraces in spider monkeys occur during uncertain situations, such as after subgroup fusion and in the context of other females' infants handling (Aureli & Schaffner, 2007; Slater, et al., 2007). Thus, one could argue that 'Security' could be an appropriate label for the second component, corresponding to

the proposed terminology for primate social relationships (Aureli & Cords, 2000) and fitting with previous studies (Fraser et al., 2008). This labelling however may not apply to spider monkeys, as although dominance relationships are extremely difficult to detect (Aureli & Schaffner, 2008), aggression occurs in a predictable fashion. The vast majority of aggressive interactions occur in three contexts: the aftermath of fusion events (Aureli & Schaffner, 2007), when females are most likely to conceive (Slater et al., 2008) and when females are new immigrants in a community (Asensio et al., 2008). As unpredictability is inherent in the definition of 'Security' (Cords & Aureli, 2000), I propose a different label for this component.

Risk is a better label to capture the high loading of both aggression and embrace rates. Aggression and embraces are associated as the latter can reduce tension and the risk of aggression in the aftermath of fusion events (Aureli & Schaffner, 2007; Chapter 4). There is further evidence that embraces serve as a signal of benign intent in contexts that are associated with risk in spider monkeys, such as access to infants (Schaffner & Aureli, 2005; Slater et al., 2007) as females with young are potentially at risk for infanticide, which has been documented at this field site (Gibson, et al., 2008). In fact, the pattern of injuries in a captive group of spider monkeys seemed to indicate that bites were given during embraces, which themselves present a risky context as the individuals exchanging embraces are 'trapped' with each other for the duration of the embrace (Schaffner & Aureli, 2005). Consequently, in spider monkeys, embrace rates are likely a highly appropriate measure of risky relationships.

Sex combination had a clear effect on Risk. Male-male dyads had more risky relationships than female-male and female-female dyads. This result confirms the ambiguous nature of male-male relationships (Aureli & Schaffner, 2008), which are characterised by the highest rates of affiliative behaviour, while simultaneously possessing a dangerous element. For example, lethal male-male aggression has been reported in spider monkeys. Lethal aggression occurred more often than expected in zoo-settings, particularly between adult males and maturing males (Davis, Schaffner & Wehnelt, 2009). Also in wild spider monkeys episodes of lethal aggression have been observed in two separate populations (including the study population) in which male-male intragroup coalitionary attacks led to the death of community younger

males (Campbell, 2006; Valero et al., 2006). The overall male to female sex ratio in adult populations, ranging from 0.22 to 1.00, is skewed more towards females than in the juvenile population (Shimooka et al., 2008). This suggests a possible dramatic fate for maturing and young adult males. Moreover, female-male dyads were less risky than male-male dyads and this may stem from a different function that aggression seems to have in mixed sex dyads. Female-directed male aggression accounted for 57% of the total aggressive interactions (Klein, 1974), and it is likely that female-directed male aggression is a form of ritualised sexual display (Slater, et al., 2008). Male-male dyads were also more risky than female-female dyads. Since among frugivorous primates females experience strong intragroup feeding competition (Sterck, Watts & van Schaik, 1997), most of the aggressive displays between females are likely contests over food. In the specific case of aggression of resident females directed to recently immigrated females, it has been proposed that it might function to discourage immigration attempts which would increase scramble competition (Asensio, et al., 2008). Such aggressive displays are unlikely to be risky since females have the opportunity to fission and search for other feeding patches, whereas the worst option for newly immigrated females is a failed immigration attempt.

The tenure of dyadic relationships also had an effect on Risk. Dyads composed of individuals who lived together in the same community for a longer time had riskier relationships. The result appears to be in contrast to what would be expected based on previous studies. A long history of social interactions should lead to more established relationships between two individuals (Brosnan, Schiff & de Waal, 2005). A possible explanation could stem from the definition of relationship tenure used in my study. Short-tenure relationships were those composed of at least one individual born or immigrated in the group after the beginning of 2003. Since male-male dyads were more risky than female-female and male-female dyads, the tenure effect may be a result of differential representation of the various sex categories. Considering that males are philopatric, and thus no adult or juvenile male immigrated into the study communities, and males born after 2003 were excluded from the analyses as they were still dependent on their mothers, all male-male dyads had long tenure. There were seven adult females in the study that immigrated in the

group after the beginning of 2003 and in turn of the 823 dyads in the population only 47 included an adult female that had short tenure

I am however left with a paradox as males have both the most compatible and the riskiest relationships with one another. This, however, is not only typical of my study and may be an effect related to the age class of males (Aureli & Schaffner, 2008). Indeed, younger males are highly attracted to older males, but may face a difficult transition when becoming full adults as there is a risk of lethal aggression from fully adult males (Vick, 2008). One behaviour that might provide insight on this paradox is grappling, in which males engage in a series of approach-retreats exchanging embraces, face greetings, and sometimes mutual genital manipulation for many minutes (Vick, 2008). A better understanding of male-male social relationships would be achieved if the effect of grappling on Risk is assessed as grappling is associated with high tension and appears to be important in developing male-male relationships (Klein, 1971; Aureli & Schaffner, 2008). Unfortunately, observations of grappling are rare and more cases are needed before an appropriate analysis can be performed.

3.4.4 Conclusions

The present study provides a further insight into the mechanisms that regulate the quality of relationships in non-human primates. Overall, the results presented here are in accordance with what is currently known about spider monkeys' social relationships. Moreover, the use of PCA led to a more detailed understanding of spider monkeys' relationships. Spider monkeys' social relationships involve at least two components of relationship quality. The components of Compatibility and Risk correspond in part to the concepts outlined in the theoretic framework for social relationships proposed by Cords and Aureli (2000). Nonetheless, the two components and their respective loadings may further contribute to understanding the factors that surround conflict and how it is managed in spider monkeys. In fact, the behavioural mechanism adopted to manage conflicts depends on the benefits entailed in any dyadic relationship and on the cost of maintaining such benefits. Finally, these components have been particularly useful in understanding male relationships, which are characterised both by a high degree of Compatibility and Risk.

Chapter 4

Post conflict interactions in wild spider monkeys

4.1. Conflicts of interest

Conflicts of interest are common in group living species, such as when members of the same community need to take different courses of action or compete over limited resources (Aureli et al., 2002; Chapter 1). When these conflicts escalate into overt aggression there are likely to be negative consequences for either one or both participants. The most direct costs of aggression are energy expenditure and occasionally physical injury (Drews, 1996; Arnold & Aureli, 2007). Further costs are less evident and remain present even after the aggression has ended. A negative outcome can result for one of the participants in the loss of a contested feeding resource (Aureli, 1992; van Noordvijk & van Schaik 1987) or sexual resource (Bercovitch, 1988). A further cost of aggressive interactions lies in the high risk for the victim to receive further aggression by the original aggressor (York & Rowell, 1988, Cords 1992; Das, et al., 1998; Kutsukake & Castles, 2001). Anxiety is another cost entailed in aggressive interactions, which can have negative health consequences over the long term (Kaplan, 1986). The risk of further aggression and the loss of access to specific resources may account for the high levels of anxiety experienced by victims (Aureli et al., 1989; Aureli 1992; Aureli, 1997; Castles & Whiten, 1998; Das et al., 1998; Schino, 1998; Schino, et al., 2007). Instead, the damage caused by aggression to the relationship of the previous opponents affects the victim and the aggressor given the loss of future cooperation (Aureli & Smucny, 2000). Indeed, the disturbance to a valuable relationship of former opponents is another cost due to aggressive interactions. Such disturbance means consequently the loss of benefits provided by the cooperation between the two partners (Aureli, 1997).

Mechanisms to deal with the costs that result from aggressive interactions have been selected to maintain the benefits acquired in group living (see Chapter 1). Aggressive interactions may have evolved within a group setting as a means to negotiate social relationships, post conflict behaviours are an adaptive response to the costs of aggression (de Waal, 2000a; Aureli & de Waal, 2000). Post conflict interactions (PCI) are behavioural mechanisms that serve the function to reduce the

cost of aggressive encounters (de Waal 2000a; Aureli, et al., 2002; Arnold & Aureli, 2007).

4.1.1 Post conflict interactions

Since reconciliation was reported (de Waal & van Roosmalen, 1979) several other forms of PCIs have been recognised, such as further aggression, third-party affiliation, and third party aggression (Wittig & Boesch, 2003; Koski, et al., 2007b). Reconciliation, defined as the friendly post-conflict reunion between former opponents (de Waal & van Roosmalen, 1979), has been reported to occur in the majority of primate species investigated (Arnold & Aureli, 2007)(see Table 1.1). Reconciliation has also been demonstrated to occur in a few studies conducted on non-primate species (wolves, *Canis lupus*, Cordoni & Palagi, 2008; dogs, *Canis familiaris*, Cools, van Hout & Nelissen, 2008; dolphins, *Tursiop,* spp., Samuel & Flaherty; 2000; Weaver, 2003; domestic goats, *Capra bircus*, Schino, 1998; spotted hyenas, *Crocuta crocuta*, Hofer & East; 2000; Wahaj, Guse & Holekamp, 2001). There is wide agreement about the main function of reconciliation, which is to repair the relationship of the two contestants (Cords & Aureli, 2000). Several studies demonstrated the validity of that hypothesis showing how partners with more valuable relationships reconcile more than partners with less valuable relationships (Kutsukake & Castles, 2001; Cooper, et al., 2005; Wittig & Boesch, 2005, Preuschoft, Wang, Aureli & de Waal, 2002). Valuable relationships imply a degree of fitness benefit for both partners and are often characterised by kin relatedness (Kappeler & van Schaik, 1992; Aureli, 1997), cooperation (Cords & Thurneer, 1993) and formation of alliances (Mitani, et al. 2000; Watts, 2006; Koski, et al., 2007a). In addition, partners with compatible relationships reconcile more frequently (Aureli, van Schaik & van Hoof, 1989; Call, Aureli & de Waal, 1999; Schino, et al., 1998; Palagi, et al., 2004). This suggests that compatible relationships, defined as the general tenor of social interactions between two individuals (Cords & Aureli, 1993; Chapter 3), are also "repairable" through reconciliation.

A further function provided by reconciliation is to reduce the anxiety levels caused by aggressive interactions in former opponents. Indeed, several studies indicate a reduction of self-directed behaviours in individuals who just engaged in reconciliation (Aureli & van Schaik, 1991b; Castles & Whiten, 1998; Das et al.,

1998; Arnonld & Whiten, 2001; Kutsukake & Castles, 2001). Reduction in anxiety can be explained at a proximate level through the effect reconciliation has in lowering the likelihood of renewed attacks between former opponents (Cords, 1992; Watts, 1995; Castles & Whiten, 1998; Koyama, 2001) and in restoring the tolerance between them (Cords, 1992; Cheney & Seyfarth, 1997). A further explanation of post-conflict anxiety is possibly due to the uncertainty about the future relationship of the former opponents (Aureli, 1997). The benefits associated with valuable and compatible relationships might be compromised by aggressive encounters and the emotional distress that results is likely to play a role in mediating reconciliation behaviour (Aureli & Smucny, 2000; Koski, et al. 2007a), because the anxiety triggers individuals to reconcile to reduce the ensuing anxious state.

The occurrence of reconciliation and other PCIs depends on several factors that influence the type of PCIs adopted and the extent to which they are used (Arnold & Aureli, 2007; Koski, et al., 2007; Wittig & Boesch, 2003). For example, reconciliation is expected to be lower in species with a tolerant dominance style (Arnold & Whiten, 2001) and in species in which the risk of physical injury is higher (Schino, 2000). Furthermore, high predation pressure should lead to an increase of reconciliation frequency (Schino, 2000). A further prediction concerns the degree of cohesiveness of a given species. The option to leave the group represents an alternative strategy to cope with the cost of aggression. Therefore, less cohesive societies may not need to rely on PCIs (Schino, 2000).

4.1.2 PCIs and fission-fusion dynamics

Chimpanzees and bonobos (*Pan* spp) are species with a high degree of fission-fusion dynamics (FF dynamics) that have received most of the attention of studies on PCIs. Reconciliation was first recognised in chimpanzees (de Waal & van Roosmalen, 1979) and was then demonstrated to occur in many other studies on the same species (Arnold & Whiten, 2001; Preuschoft et al., 2002; Fuentes, Malone, Sanz, Matheson & Vaughan, 2002, Wittig & Boesch, 2003; Koski et al., 2007a; Fraser & Aureli, 2008) and on closely related bonobos (de Waal, 1987; Hohman & Fruth, 2000; Palagi et al., 2004). Bystander affiliation was also found in chimpanzees (de Waal & van Hooff, 1981, Arnold & Whiten, 2001; Wittig & Boesch, 2003; Kutsukake & Castles, 2004; Palagi, Cordoni, Borgognini, Tarli, 2006; Fraser &

Aureli, 2008; Fraser et al., 2009; Koski & Sterck, 2009) and bonobos (Palagi, et al., 2004). Redirection and renewed aggression are other PCIs demonstrated in *Pan* (redirection: Fuentes et al., 2002; Koski, et al., 2007b; Wittig & Boesch, 2003; renewed aggression: Wittig & Boesch, 2003). Furthermore, in a few other non-primate species with social organisations characterised by a high FF dynamics reconciliation has been documented. In bottlenose dolphins former opponents approached each other and engaged in affiliative interactions, such as gentle rubbing and swim in contact (Samuel & Flaherty, 2000). Spotted hyenas reconcile through partner licking and groaning (Hofer & East, 2000; Wahaj, et al., 2001) and evidence of reconciliation, as well as renewed aggression, is provided for goats (*Capra aegagrus hircus*, Schino, 1998). Moreover, Poole and Moss (2008) report that elephants used vocal displays to reconcile and that such behaviour usually involved third parties.

4.1.3 Fission as a PCI

In social organisations with high degree of FF dynamics, the opportunity to fission from former opponents has rarely been included as a behavioural strategy to take into account in the analysis of PCIs. Furthermore, a captive study setting, in which the majority of post-conflict studies have been carried out, may preclude animals from expressing their full behavioural repertoire, i.e. it may not be possible to observe fission even if it is a species-specific behavioural strategy to cope with the aftermath of aggression. Information regarding the occurrence of fission from a former opponent as a PCI is largely anecdotal and has not been statistically verified. Wild chimpanzees rarely fissioned from each other after a conflict (Arnold & Whiten, 2001), although the authors did take into account the possibility of fission as a PCI. In addition, spotted hyenas seem to fission from the opponent's subgroup in response to aggression following approximately 20% of fights, and the tendency to fission was lower when former opponents had reconciled (Smith, Kolowski, Graham, Dawes & Holekamp, 2008).

4.1.4 Aims of the study

The aim of the present chapter was to contribute to the understanding of spider monkeys' post-conflict mechanisms. First, I characterised the patterns of aggression in two wild communities of spider monkeys. Second, I investigated whether aggressive interactions led to an increase in anxiety. Third, I explored which PCIs were employed by the spider monkeys in the aftermath of aggression, including reconciliation, bystander affiliation, redirection of aggression, and fissioning. Finally, I analysed whether PCIs are influenced by components of relationship quality.

4.2 Methods

4.2.1 Subjects

Data were collected on all the adult and juvenile members that were more than three years of age from the two communities that were involved in aggressive interactions. In the Eastern community I collected data on eight of the 11 adult individuals and three juveniles (five adult females, three adult males, two juvenile males and one juvenile female), whereas in the Western community I collected data on only seven individuals including one adult male, two adult females, one juvenile female and one juvenile male. As relatively few aggressive interactions were collected during my second observation season in 2006 (see Chapter 2, Table 2.2), I supplemented the data with focal observations extracted from a dataset on the same communities of spider monkeys during the years 2003 and 2004. In the Eastern community, data were extracted for nine focal individuals (four adult males and five adult females) and on five individuals in the Western community, including two adult males, one adult female and two juvenile males.

4.2.2 Procedure

Post conflict observations (PCs) were collected on all individuals involved in aggressive interactions, victims and aggressors. PCs started immediately after an aggressive encounter. To analyse whether reconciliation and bystander affiliation occurred, friendly behaviours including grooming, contact and proximity were recorded as all occurrence. Since self-directed behaviours, such as scratching, self touching and self grooming reflect levels of anxiety (Maestripieri, et al.,1992;

Schino, et al., 1996; Barros, Boere, Huston & Toaz, 2000) and have been used previously to measure anxiety in former opponents (Aureli, 1992; Aureli et al., 1989; Aureli, 1997; Castles & Whiten, 1998; Das et al., 1998; Schino, 1998; Schino, et al., 2007), I recorded scratching on an all occurrences basis. Further aggressive events were recorded to analyse the occurrence of redirection and aggression given and received by former opponents. All fission events were also recorded to investigate the latency to fission following aggressive episodes (see Chapter 2, section 2.5). Matched-control observations (MCs) were selected from focal observations based on the following criteria: 1) no aggression had occurred prior to the MC since commencing the subgroup follow; 2) the two opponents were present in the same subgroup; 3) the subgroup composition matched as close as possible the PC subgroup composition and 4) the closest focal in time with the three previous characteristics was selected.

4.2.3 Statistical Analyses

Aggression rates were obtained by dividing the number of conflicts two individuals were involved in by the total time spent together in the same subgroup. Dyads that spent less than 1 hour of time together were excluded from the analysis. I performed two linear mixed model tests (LMMs) to examine the effect of sex, age, tenure and community membership on the rate of aggression per hour that individuals received (victims) and that individuals gave (actors). The best model was selected based on Akaike's criterion.

To calculate rates of post-conflict scratching I summed the number of scratches at the individual level and divided it by the total time in view throughout the PCs of the same focal individual. To determine whether scratching rates were subjected to an immediate and short effect of post-conflict anxiety, I calculated scratching rates during the first five minutes of a PC. I assumed that the scratching rate during the MCs would reflect a baseline rate of scratching. Therefore, as matched control for scratching rates during the entire 15 minutes of the PC and during the first five minutes of the PC I used the scratching rates of the entire corresponding MCs. PCs and MCs taken in "wet" conditions (just after rain) were excluded from the analysis, as the monkeys are known to scratch at high rates when they are wet.

In order to analyse the data for post-conflict affiliation PC-MC pairs were analysed with the PC-MC method to determine the occurrence of affiliative behaviours, including reconciliation and bystander affiliation (de Waal & Yoshihara, 1983). PC-MC pairs were labelled as early pairs if the first affiliative interaction between former opponents occurred earlier in the PC. If the first affiliative interaction occurred earlier in the MC the pair was labelled as late. Proportions of early and late pairs were calculated at the individual level for PCs and MCs and tested for difference across all the individuals.

To determine post-conflict aggression, the occurrence of aggressive interactions received and given by former opponents was conducted with the PC-MC method following the same procedure as for post-conflict affiliation. For all PC-MC analyses, in cases where the measures did not violate the assumption of normality (Siegel & Castellan, 1992), analyses were performed with paired t-tests, whereas when the assumption of normality was violated comparisons were performed with a Wilcoxon sign rank tests. As all Ns for Wilcoxon tests were less than 15, I reported the T value (Siegel & Castellan, 1992). To control for the inflation of alpha when multiple tests were performed on datasets that had dependency Bonferonni's correction was applied.

For analyses pertaining to post-conflict fission I made the assumption that changes in subgroup composition were always recorded (see Chapter 2, section 2.5). Therefore, for the analysis of fission latency after a conflict I enlarged the dataset with data from all occurrence observations (Chapter 2, section 2.5). A Kaplan-Meier survival analysis with a Mantel-Cox test was performed to determine whether there was a difference in fission latency of former opponents in the aftermath of a conflict compared to MCs across the duration of the whole length of the observation (Chan, 2004). The survival analyses permitted the inclusion of censored observations in the PCs and MCs in which no fission occurred before the end of observation. The time window for different fission times in PCs and MCs was used in conjunction with the PC-MC method in the following way: in a dyad when both PCs and MCs were longer than the defined time window the pair was considered neutral. PCs or MCs with censored observations before the defined time window were compared with corresponding time length in the matching PCs or MCs. PC-MC pairs where fission

occurred earlier in the PC were labelled early pairs; when fission occurred earlier in the MC the pair was labelled late. In a pair when both PC and MC were censored before the defined time window the pair was also considered neutral.

A LMM approach was applied to examine the effect of relationship characteristics, including kinship, sex composition of dyad, compatibility and risk (Chapter 3) on fission latency in the aftermath of a conflict. LMM was applied to two measures of fission latency: 1) 'PC latency' in which PC fission latency was obtained by eliminating the PCs with censored observations before one hour of time. PCs where fission times lasted longer than one hour were considered as one hour of fission latency; 2) 'PC latency relative to MC' in which the PC fission latency was considered relative to the MC average fission latency per dyad (PC latency minus average MC latency) to control for different baseline levels of fission across dyads. For both measures of fission latency I excluded two dyads composed of only juveniles. For all statistical analyses an alpha of ≤ 0.05 was set as the significance level, with the exception of those tests that were further subjected to Bonferonni's correction.

4.3 Results

4.3.1 Actors and victims of aggression

A LMM was performed to examine the factors affecting the hourly rate of aggression by actors (Table 4.1). The best model included community, age of actor, sex of actor and tenure of actor as fixed factors and actor identity as the random factor (see Table 4.2). Sex was the only significant factor in the model (Table 4.2) with males performing significantly more aggression per hour (M =0.03±0.01) than females (M = 0.001 ± 0.008).

Table 4.1 Predictors used for LMM for the factors affecting the rate of aggression by the actors and victims.

Fixed factors	Sex, age, kinship, tenure and community
Random factor	Actor identity
Dependent factor	Hourly rate of aggression

Table 4.2 Results of the best LLM model for the factors affecting the rate of aggression by the actors.

Independent variables	β	SE	t value	p value	95% low and high confidence intervals
Sex (F-M)	-.001	.016	-2.61	.013	-0.03 – -0.5
Community (Western-Eastern)	.02	.01	1.70	.10	-.004 – .04
Age (Adult –Juvenile)	.01	.01	1.04	.28	-.001 – .03
Tenure (Long-Short)	.02	.01	1.84	.086	-.002 – .04

A further LMM was then performed to examine the factors affecting the rate of aggression received by victims. The best model included community, age of victim, sex of victim and tenure of victim as fixed factors and victim identity as the random factor (Table 4.3). Sex was the only significant factor in the model with males receiving more aggression per hour (M =0.02±0.008) than females (M = 0.002 ± 0.006).

Table 4.3 Results of the best LMM model for the factors affecting the rate of aggression per hour received by victims.

Independent variables	β	SE	t value	p value	95% low and high confidence intervals
Sex (F-M)	-.02	.008	-2.30	.025	-0.02 – 0.4
Community (Western-Eastern)	.01	.008	1.27	.26	-.008 – .03
Age (Adult –Juvenile)	.01	.008	1.34	.19	-.006 – .03
Tenure (Long-Short)	.001	.01	.09	.927	-.02 – .02

4.3.2 Post-conflict scratching

I had 67 PC-MC pairs on 25 individuals and involving 55 different opponent dyads. I tested for differences in scratching rates between PCs and MCs to determine if aggression led to anxiety in the former opponents. Scratching rates in the entire 15 minutes of the PCs were not different from those in the entire MCs [actor and victim together: $t(23)$=.85, p=.40; victim: $t(17)$=1.13, p=.27; actor: $t(9)$=.48, p=.64; Table 4.4]. When only the first 5 PC minutes were considered, there were no differences

for actors and victims together [$t(23)=1.91$, $p=.07$] or for actors only [$t(9)=.83$, $p=.43$]. However, victims' scratching rates in the first 5 PC minutes were significantly higher than those in the entire 15 minutes of the corresponding MCs [$t(17)=2.94$, $p=.009$; Figure 4.1].

Table 4.4 Mean (±SE) scratching rates during the entire 15 minutes of PCs and MCs.

Former opponent(s)	PC	MC
Actor and victim	.2747 ± .03284	.2346 ± .03698
Victim	.3080 ± .03791	.2475 ± .04543
Actor	.2078 ± .04951	.1682 ± .04618

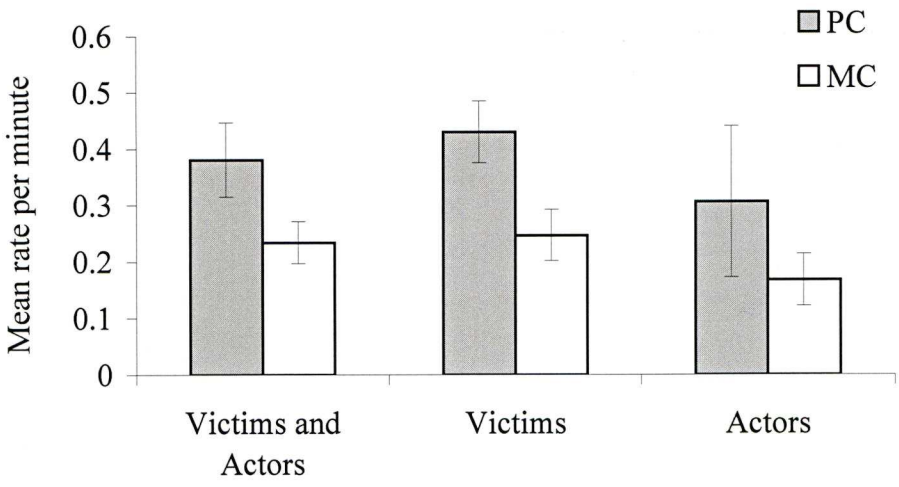

Figure 4.1. Mean (±SE) scratching rates per minute in the first 5 PC minutes and in the entire 15 MC minutes for aggressors and victims together, only victims and only aggressors. * = significant difference between PCs and corresponding MCs.

4.3.3 Post-conflict affiliation

Only three affiliative contacts between opponents occurred in the 67 PCs and one in 67 MCs. Using the PC-MC method at the individual level, there was no difference in the proportion of early and late pairs (ties=21, $n=4$, $T=1$, $p=.25$; Table 4.5). Therefore, I found no evidence for reconciliation. In addition, there were seven and 13 episodes of bystander affiliation in PCs and MCs, respectively. However, there was no significant difference in the proportion of early and late pairs (ties=13,

n=12, T=31 p=.56; Table 4.4). Therefore, I found no evidence for bystander affiliation.

Table 4.5 Mean (±SE) of early and late pairs for affiliation between opponents and bystander affiliation.

Type of PC affiliation	Early pairs	Late pairs
Affiliation between opponents	.0313 ± .01775	.0057 ± .00571
Bystander affiliation	.1470 ± .05960	.2021 ± .06397

4.3.4 Post-conflict aggression

There was no evidence for post-conflict aggression. Neither actors of aggression nor victims received any aggressive interactions in the PCs, although three aggressive interactions were received in the MCs. There was no significant difference in the proportions of early and late pairs (ties= 21, n= 3, T=0, p= .25; Table 4.6). Therefore, former opponents did not receive more aggression following a conflict compared to MCs. When I examined the data for evidence of redirection of aggression, I found only one post-conflict aggressive interaction by the actors and one by the victims in the PCs, whereas none occurred in the MCs .There was no significant difference in the proportions of early and late pairs (ties=23, n=2, T=0 p=.50; Table 4.6). Therefore, I found no support for redirection of aggression.

Table 4.6 Mean (±SE) of early and late pairs for aggression received by and redirected by the focal individual.

Type of post –conflict aggression	Early pairs	Late pairs
Received	.00 ± .00	.05 ± .03
Redirected	.04 ± .04	.00 ± .00

4.3.5 Post-conflict fission

For the following analyses data from PC-MC pairs were supplemented with data from all occurrences in which appropriate control periods were identified for each post-conflict period. Hereafter, they are all labelled as PCs and MCs (N=85). Forty-one and 31 fissions of former opponents were observed following a conflict (PCs) and in baseline observations (MCs), respectively. The latency for fission was shorter in the PCs than in the MCs [survival analysis Mantel-Cox: $\chi^2(1)$=4.73 p=.03].

A window of 3600 seconds was identified as the time period in which the slopes of the two lines differed (Figure 4.2).

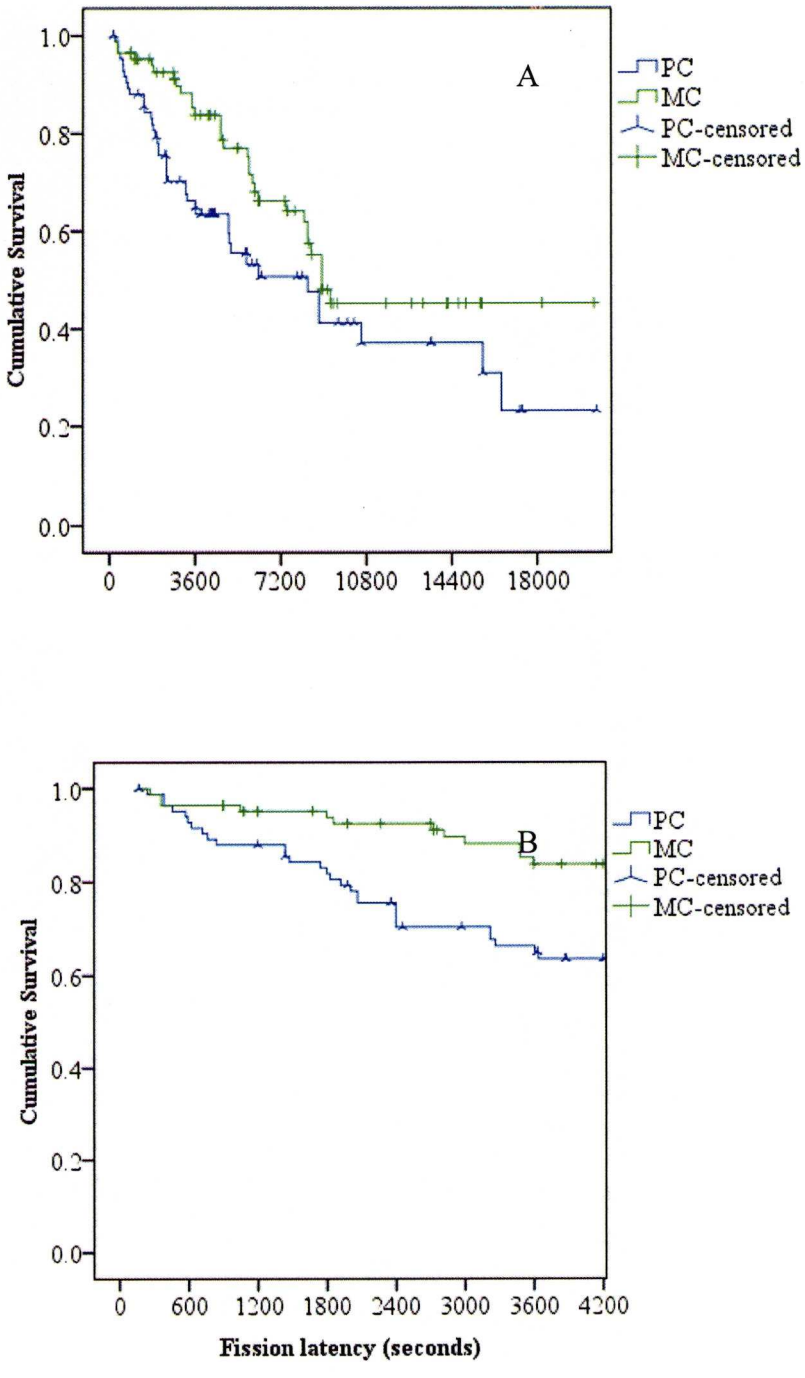

Figure 4.2 A) Shows the latency to fission across the entire observation period in the PC and the MC; B) Shows the latency to fission during the first 3600 seconds, which was identified as the meaningful interval, and the latency was shorter in the PC than the MC for all observations and the slopes of the two lines are significantly different.

A Wilcoxon signed rank test confirmed at the individual level that spider monkeys were more likely to fission from former opponent within 3600 seconds from the beginning of a PC than from the beginning of a MC (ties=8, n=10, T=7, p=.037; Figure 4.3).

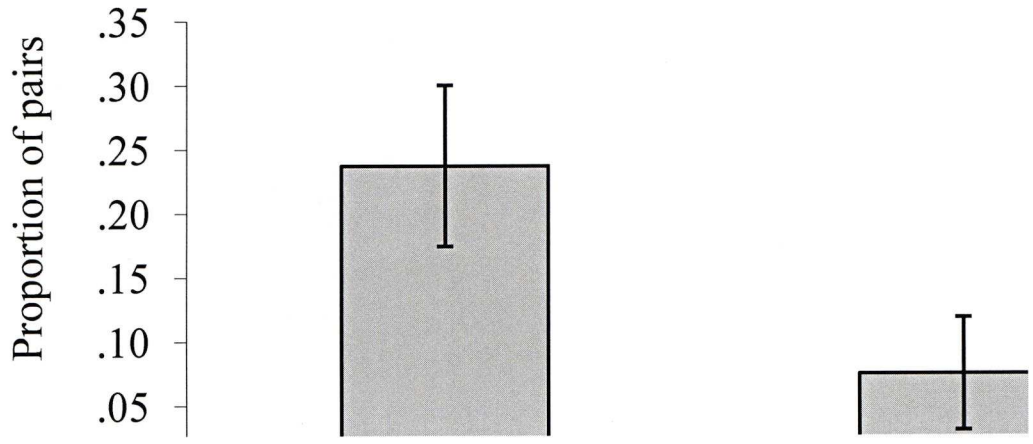

Figure 4.3. Mean (±SE) proportions of early and late pairs for fission latency within 3600 seconds from beginning of PCs and MCs.

A LMM was then performed to identify the best model explaining the patterns of PC fission latency and included kinship and compatibility as fixed factors, and the random variable was partner 1 (Table 4.7). The random variable 'partner 2' did not contribute any variance, and was therefore excluded as a random factor from the best model. The effect of compatibility approached significance. More compatible partners tended to fission later than less compatible partners (Table 4.8). Kinship did not influence PC fission latency as dyads comprised of kin (n=3) fissioned at nearly the same number of seconds (M=2880.0 ±720.0) as did non-kin (n=71, M=2894.4 ±131.2).

Table 4.7 Predictors used for LMM of the effect of relationship characteristics on PC fission latency.

Fixed factors	Kinship and compatibility
Random factor	Partner identity
Dependent factor	PC fission latency

Table 4.8 Results of the best LMM indicating the influence of relationship characteristics on PC fission.

Independent variables	β	S.E.	t value	p value	95% confidence intervals
Intercept	2957.35	152.84	19.35	.000	2626.81–3287.88
Compatibility	584.69	314.67	1.86	.068	-43.84–1213.10
kin – non kin	-1715.90	1128.61	-1.52	.133	-3969.71–537.91

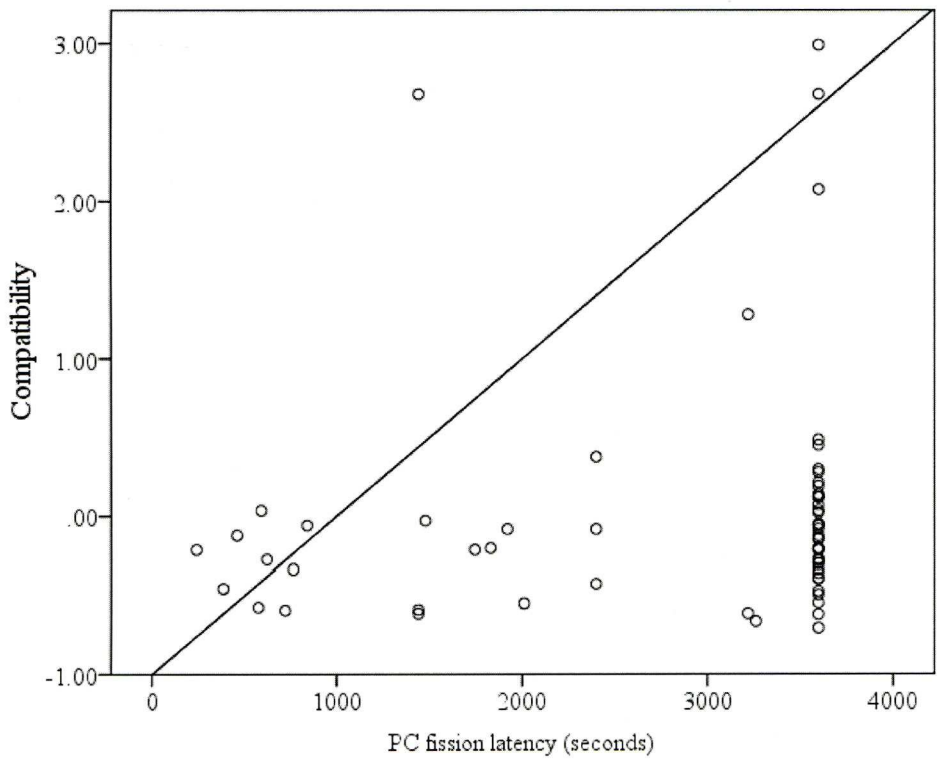

Figure 4.4. Illustrates the relationship between the compatibility rating from the PCA as a function of the post conflict fission latency.

To control for different baseline levels of fission across dyads, I ran a LMM using PC fission latency relative to MC average fission latency per dyad of individuals as the dependent variable (Table 4.9). The best model explaining the patterns of PC fission latency relative to MC average fission latency per dyad of individuals included sex combination, kinship, compatibility and risk as fixed factors (Table 4.10). The random factors, partner 1 and partner 2 did not contribute any variance, and were therefore excluded from the best model. I found that male-male

dyads fissioned significantly sooner in the PCs relative to the MCs than female-male dyads fissioned, whereas there were no differences between the other sex combinations (Figure 4.10). The effect of compatibility and kinship approached significance. More compatible partners tended to fission later in the PCs relative to the MCs than less compatible partners (Figure 4.10). Similarly, kin tended to fission later in the PCs relative to the MCs than non-kin (mean±SE for kin (n=3)= 720.00±720.00 and for non-kin(n=61)= 403.44±174.09.).

Table 4.9 Predictors used for LMM on the effects of relationship characteristics on the PC fission latency relative to MC average fission latency.

Fixed factors	Kinship and compatibility
Random factor	-
Dependent factor	PC fission latency relative to average MC

Table 4.10 Results of the best LMM indicating the influence of relationship characteristics on the PC fission latency relative to MC average fission latency.

Independent variables	β	SE	t value	p value	95% confidence intervals
Sex (FF-MM)	526.14	463.89	1.13	.261	-402.79 – -301.50
Sex (FM-MM)	988.69	435.65	2.27	.027	116.32 – 1861.05
Sex (FM-FF)	462.55	365.06	1.27	.210	-268.47 – 1193.57
Compatibility	655.75	358.94	1.83	.073	-63.02 – 1374.53
Risk	98.06	96.09	1.02	.312	-94.36 – 290.48
Kinship	-2181.14	1263.94	-1.73	.090	-4712.15 – 349.86

MM, male–male dyads; FM, female–male dyads; FF, female–female dyads.
Only variables present in the best model are shown.
To compare FF vs. FM data, the model was rerun, altering the order of the levels.

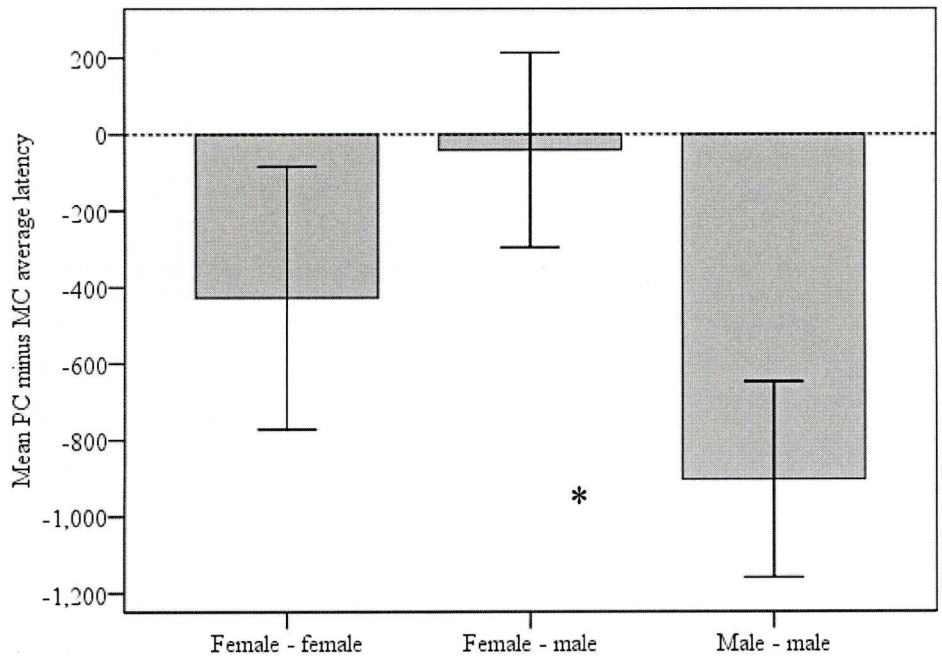

Figure 4.5: Mean ± SE for female-female, female-male and male-male dyads. * = significant difference between female-male and male-male dyads.

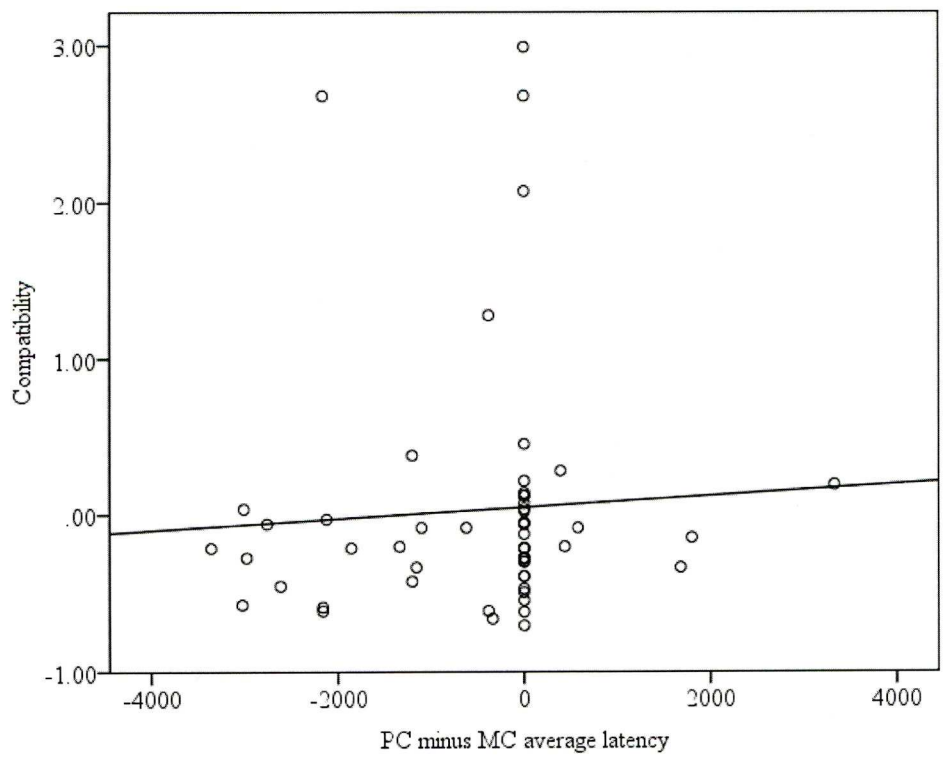

Figure 4.6. Illustrates the relationship between the compatibility rating from the PCA as a function of the post conflict fission latency relative to MC average fission latency.

4.4 Discussion

In the present study, I investigated aggressive behaviour and its aftermath with the primary aim of determining what behavioural strategies spider monkeys used to cope with aggression. In addition, I examined the extent to which components of spider monkeys' social relationships influenced the expression of the PCIs. I demonstrated that victims of aggression experienced increased anxiety immediately following the receipt of aggression. However, spider monkeys from the two communities I studied did not show any of the following PCIs: reconciliation, bystander affiliation or redirected aggression. Instead, fission between former opponents was significantly more likely to occur within one hour after a conflict than in MCs. Furthermore, more compatible partners tended to fission later than less compatible partners, male-male dyads fission significantly sooner than male-female dyads and more compatible partners and kin tended to fission later in the PCs relative to the MCs than non-kin.

4.4.1 Pattern of aggression

In the two communities studied, hourly aggression rates analysed with LMM showed that males performed and received significantly more aggression compared to females. This result is in contrast with what has been reported from other studies on wild spider monkeys. The most frequent direction of aggression reported for wild spider monkeys is adult males targeting adult females (Fedigan & Baxter, 1984; Campbell, 2003, Slater, et al., 2008), whereas intra-community aggression between males is reported to be rare (Fedigan & Baxter, 1984; Aureli & Schaffner, 2008). However, intragroup coalitionary lethal aggression occasionally occurs between males (Valero et al., 2006; Campbell, 2006). Furthermore, one captive study, involving a survey of the patterns of aggression in 32 zoos, revealed that disproportionately more aggression is directed by adult males toward younger males than toward other age-sex categories (Davis, et al., 2009). The results obtained from my study subjects could be explained by three factors. First, the higher aggression rates found for male-male dyads compared to other sex combinations may be due to the context in which they were observed. I was often observing subgroups

comprised of females and their young, when a subgroup of males joined. Typically, the males from the joining subgroup were aggressive towards the encountered group members, and then rapidly fissioned. Thus, it is possible that the aggression displayed was related to fusion events, which are frequently accompanied by aggressive behaviour (Schaffner & Aureli, 2007; Chapter 5). It is possible therefore that the rate of aggression per hour is inflated by the specific high tension circumstances in which data on males was often recorded. While this explanation may account for a higher rate of aggression displayed by males, it does not account for why other males should be selectively targeted.

The second factor that affected the rate of aggression can be related to hurricanes Emily and Wilma, which occurred near the end of the first season of my data collection. The hurricanes affected the availability of high quality resources, which the monkeys rely on for over 70% of their diet (see Chapter 6). In turn, the dramatic decrease of food resources led to an increase in the inter-birth interval for females (Vick, Schaffner, Ramos-Fernandez & Aureli, unpublished data), which has been documented in other species when females experience a decline in aspects of their habitat quality (Lee & Hauser, 1998; Cheney, Seyfarth, Fischer, Beehner, Bergman et al. 2004). In spider monkeys, the vast majority of aggression that males direct toward females occurs during periods of time when females are most likely to conceive (cf Slater et al., 2008), thus the proportion of aggression directed toward males could be greater during the second field season, which occurred in the aftermath of two hurricanes and females did not appear to cycle during this period.

The third factor that might have contributed to create a high aggression rate for males is that a disproportionate amount of the aggression in the Western group was directed by older males toward juvenile males. One explanation that has been forwarded to account for male-male lethal aggression is that when the sex ratio of females to males, which is at least approximately 2:1 in most wild populations (Shimooka et al., 2008), approaches a ratio of 1:1, it serves as a proximate trigger for aggression by older males toward maturing males (Valero et al., 2006). At the time of my observations the number of juvenile males in the Western community was high (n = 6) relative to the adult males (n=7) and when including juvenile males in the adult sex ratio it was 1.07:1, compared to 2.29:1 without considering the

juvenile males. There was however an even greater number of juvenile females in the community (n=9), which maintains the skew at 1.92:1, although the juvenile females are highly likely to emigrate from the group when reaching reproductive maturity (Vick, 2008). Thus, the prevalent pattern of aggression within spider monkey communities may be context specific and change over time. Thus, in periods of time when several females are likely to be receptive, males may target more aggression toward adult females than other age-sex classes (Slater et al., 2008), but when there are a high number of males relative to potentially reproductive females intra-community competition among males may be the more prevalent pattern.

4.4.2 Post-conflict anxiety

When I examined evidence for anxiety in the aftermath of aggression, I found that scratching rates were significantly higher during the first five minutes of PCs compared to MCs. This result applied only to the victims of aggressive interactions, whereas no difference in scratching rate was found for aggressors. Increase in victims' anxiety levels during post-conflict observations has been demonstrated previously (Aureli, et al., 1989; Aureli & van Schaik, 1991b; Kutsukake & Castles 2001; Castles & Whiten, 1998), and is attributed to the uncertainty of renewed attacks (Aureli, et al., 1989) and to the potential loss of benefits related to the quality of the relationship between former opponents (Aureli, 1997; Das et al., 1998). The lack of a difference in scratching rates in actors of aggression between PCs and MCs suggests that actors are unlikely to receive post-conflict aggression from the victim and may also indicate a low relationship value of the dyads involved in aggressive encounters. Alternatively, there might be an asymmetry in the damage to the relationship experienced by former opponents (Koski et al., 2007a). For example, younger males may experience greater costs from aggressive conflicts directed by older males in terms of a lack of cooperation.

4.4.3 Post conflict interactions

Reconciliation did not occur in my study subjects as only a small number of affiliative interactions between former opponents were displayed during PCs and those were not significantly different from MCs. No information about reconciliation in spider monkeys is available to date. However, my study is not the first to fail to

find reconciliation in non-human primates (tamarins, *Saguinus labiatus*: Schaffner & Caine, 2000; lemurs, *Lemur catta*: Kappeler 1993; *L. macaco*, Roeder, Fornasieri & Gosset, 2002). In tamarins, the function of reconciliation, to repair social relationships, is thought to be unnecessary given that the tight social bonds between the individuals that were involved in aggression were unlikely to be disrupted by the mild nature of the aggressive conflicts. The reason lemurs do not reconcile is that aggressive interactions are limited to individuals with low quality relationships (Kappeler, 1993; Roeder et al., 2002). Indeed, among the prerequisites for reconciliation to occur is that the relationship of at least one opponent must be compromised by the aggression (Aureli, et al., 2002). The majority of conflicts in my dataset occurred in dyads with potentially poorer relationship qualities, such as non-kin and dyads with low compatibility. It is plausible that the relationships between those opponents were not disturbed by aggression and therefore PCIs to repair the relationships were not required. Furthermore, there was asymmetry in the perceived damage to the relationship, as illustrated by elevated post-conflict scratching rates in victims, but not aggressors, which supports the hypothesis that relationships between former opponents are not equally compromised by aggressive conflicts. Therefore, it might not pay to engage in reconciliation and incur a risk of renewed hostility when the benefit of reconciliation is not equal between the opponents (Aureli, et al., 2002). Finally, it is possible that post fusion aggression is not reconciled as it might not disrupt social relationships as reported for aggression occurring during feeding contexts (Aureli, 1992; Verbeek & de Waal, 1997).

Bystander affiliation was also not demonstrated in the present study. Klein and Klein (1971) described episodes of bystander affiliation directed to victims in captive spider monkeys. I observed seven cases, but they were insufficient to provide statistical support. The occurrence of bystander affiliation in species with no evidence for reconciliation is quite uncommon. A study conducted on rooks (*Corvus frugileus*) (Seed, Clayton & Emery, 2007) reports that bystander affiliation was used as a PCI, whereas reconciliation was not demonstrated. The explanation provided was that reconciliation did not occur because aggression between valuable partners never happened, whereas bystander affiliation served to reduce stress and strengthen bonds between one opponent and a bystander. Bystander affiliation may also function for third parties as a self-protection from further aggression of opponents

(Koski & Sterck, 2009). However, other findings suggest that bystander affiliation after a conflict might be used as an alternative mechanism to reduce anxiety and repair relationships between opponents when reconciliation is not performed (Watts, Colmenares & Arnold, 2000; Arnold & Barton, 2001; Wittig & Boesch, 2003; Witting et al., 2007; Fraser et al., 2009).

Redirected aggression may buffer the effect of aggression-induced anxiety in one of the opponents (Wittig & Boesch, 2003) and renewed aggression received by former opponents may occur when the outcome of an aggressive conflict is unexpected and losers have a sufficient likelihood of winning or winners need to reaffirm their dominant position (Wittig & Boesch, 2003). Thus, the failure to demonstrate redirected or renewed aggression in this study can be interpreted as the original aggressive interactions did not produce the condition to make the use of redirection worthwhile. Given that neither reconciliation nor bystander affiliation occurred in the present study the most likely explanation is that valuable relationships were not disrupted by aggression. Furthermore, the absence of redirected aggression may support the hypothesis that the aggressive interactions were not perceived as disrupting the social relationships of former opponents.

In the present study, spider monkeys who engaged in aggressive interactions were more likely to fission from each other within one hour from the aggressive event compared to MCs. In species living in social organisations characterised by a high FF dynamics, the use of fission as a further PCI mechanism has not been extensively investigated. One reason is that most studies on relevant species have been carried out in a captive setting (de Waal & van Roosmalen, 1979; de Waal, 1987; Preuschoft, et al., 2002; Fuentes, et al.,, 2002; Palagi, et al., 2004; Koski, et al., 2007; Fraser & Aureli, 2008). Only one study on wild chimpanzees took into account the possibility of fission in the aftermath of a conflict. Arnold and Whiten (2001) reported that victims of aggression rarely left the aggressor's subgroup in the aftermath of a conflict, although this assertion lacks of any scientific confirmation. In another study on wild chimpanzees avoidance was included in PCIs, but not fission (Wittig & Boesch, 2003).Wild spotted hyenas, which also live in societies characterised by a high fission-fusion dynamic, are found to occasionally fission

from former opponents in the aftermath of a conflict, but no statistical testing was done (Smith, et al., 2008).

The option that former opponents have to fission in the aftermath of a conflict presents benefits. Splitting from the former opponent's subgroup permits victims to avoid renewed aggressive interactions. As a consequence, post-conflict anxiety related to the risk to incur further aggression may be reduced. The possible costs entailed in fissioning from the former opponent are the loss of the monopolisable resource and the impossibility to repair the damage caused to the relationship. However, the cost of losing access to a feeding resource might be of little importance if they can exploit other food patches in the new subgroup (McFarland, 1986; Chapman, 1990; Couzin, 2006). Furthermore, in my study, the relationship between former opponents was likely of low value given that only victims experienced post-conflict anxiety and no reconciliation occurred. Therefore, if valuable relationships are not compromised and the resources are easily replaced through the exploitation of other food patches, then fission is a rather convenient strategy to cope with post-conflict uncertainty. The timing of fission events may be longer than for other PCIs, which occur within a few minutes of the conflict (Kappeler & van Schaik, 1992; Arnold & Aureli, 2007), because individuals may be reluctant to leave the subgroup on their own and need to either recruit other subgroup members or await the opportunity to join others that are fissioning

In the present study less compatible opponents tended to fission sooner than more compatible opponents in the aftermath of aggressive interactions. Previous studies demonstrated that compatibility positively influences the likelihood to reconcile (chimpanzees: Preuschoft, et al., 2002; only among male dyads in Arnold & Whiten, 2001; other primates: Cords & Aureli, 1993; Castles, Aureli & de Waal, 1996; de Waal & Ren, 1988). However, less compatible relationships may not need to be repaired since the benefit gained from such relationships is likely small. Thus, if repairing the damage to the relationship via reconciliation is not a feasible option, then less compatible individuals might choose the option to split from the former opponent.

Interestingly, male-male dyads were more likely to fission sooner in the aftermath of a conflict compared to male-female dyads. This result is in line with

what is known about male-male relationships in spider monkeys. Male-male dyads are characterised by strong bonds due to their cooperation in many tasks, such as defence of territory and females from neighbouring communities (Shimooka, 2003; Wallace, 2001; Symington, 1990). However, despite the highly affiliative behaviours reported among males (Slater, et al., 2009), they also engage in the riskiest aggressive interactions (Campbell, 2006; Valero, et al., 2006; Vick, 2008). The highly risky aspect of male-male relationships, as confirmed in the present study (see Chapter 3), justifies the shorter latency for fission between former opponents after a conflict.

In my study female-female and male-female dyads did not figure among the most compatible relationships. Neither did they figure among the most risky relationships (Chapter 3). Thus, for female-female and male-female dyads fissioning from the subgroup may not be needed when the aftermath of a conflict is not risky, considering that simple avoidance may function to cope with anxiety (Aureli, van Schaik, et al., 1989). Indeed, most female-directed male aggression likely represents a form of a sexual display, which does not undermine the quality of the relationship of the opponents (Slater, et al., 2009). In addition, female-female aggressive interactions include cases of aggression displayed by resident females towards newly immigrated females in a possible attempt to discourage immigration as a result of contest competition (Asensio, et al., 2008). Therefore, these types of aggressive encounters do not need to be repaired given that among resident and recently immigrated females relationships are likely not valuable. Conversely, male-male dyads were the most compatible and most risky (Chapter 3). In the aftermath of a conflict, fission is likely to occur among this type of dyad, when the risk is too high for victims to stay in the subgroup with the former opponent.

4.4.4. Conclusions

My study is one of the few that does not find evidence for reconciliation among former opponents, but it is the first to demonstrate post-conflict fission as a possible mechanism of conflict management. Spider monkeys do likely possess the abilities to reconcile or use other PCIs (de Waal & Yoshihara, 1983; Castles 2000), but they engage in these behaviours only rarely, when the benefits of reconciling outweigh the costs (cf, Aureli et al., 2002). This is partially because they have the

option to fission. Studies of PCIs in captive spider monkeys might shed light on this view. In a captive setting individuals need to stay together in the same enclosure (i.e. no fission is possible), therefore other PCIs might be used as an alternative way to manage conflicts.

Chapter 5

Post-fusion behaviour and relationship characteristics

5.1 Aggressive and friendly behaviours at fusion

There are a number of conflict management mechanisms that serve to prevent aggression or repair the damage to relationships in the aftermath of aggression (Aureli, et al., 2002; Chapter 1). The use of conflict management mechanisms, to reassure one another when familiar individuals reunite after a period of separation, has received relatively little research attention. This is somewhat surprising given the reunion context is likely associated with high uncertainty. Furthermore, an increase in aggression has been reported during reunions in chimpanzees (*Pan troglodytes*: Bauer, 1979; Bygott, 1979; Goodall, 1989) and in spider monkeys (*Ateles* spp: Klein & Klein, 1971; Aureli & Schaffner, 2007). Numerous species engage in affiliative behaviours when meeting after a temporary separation. Such behavioural displays are species-specific and are referred to as greetings (Colmenares, et al., 2000). In capuchin monkeys mounts and wheeze dances occurred following the reunion after a participant's absence from the group (Manson, et al., 1997; Manson & Perry, 2004). Chimpanzees groomed each other in the reunion context (Bauer, 1979) and engaged in affiliative interactions such as embraces and kisses (Bygott, 1979; Nishida, et al., 1999; Okamoto, et al., 2001). Wild woolly spider monkeys (*Brachyteles arachnoides*) engaged in highly ritualised gestures that included embraces and chuttering calls during the reunion context (Milton, 1984). In spider monkeys individuals temporarily separated typically embrace each other in a reunion context (Klein & Klein 1971; Schaffner & Aureli, 2005; Aureli & Schaffner, 2007). Greeting behaviours are also used by hamadryas baboons (*Papio hamadryas hamadryas*) in the reunion context (Colmenares, et al., 2000). Among non-primate species, spotted hyenas (*Crocuta crocuta*) also engaged in affiliative behaviours defined as greetings. Spotted hyenas that came together after a period of separation performed greetings displays that consisted of reciprocal scent inspection (East, et al., 1993). Greeting ceremonies also occur in non-mammalian taxa as wild seahorses (*Hippocampus whitei*) who greet one another when monogamous pairs reunite after a period of

separation and butterfly fish (*Chaetodon, ssp.*) use greetings after a period of separation (Vincent, 1995; Yabuta, 2002).

5.1.1 Possible functions of greeting behaviours during reunions

The occurrence of aggressive and affiliative displays following a period of separation between individuals from the same community suggests that there is uncertainty during the reunion contexts. Every encounter between conspecifics likely induces either a response of aggression or escape (fight-flight) in the motivation system of the joiners (Yabuta, 2008), therefore agonistic displays are likely in the reunion contexts, which play a role in increasing uncertainty or anxiety between joining individuals. One proposed function of greeting behaviour is to gain "assessment" time to recognise the encountered conspecific. This way the uncertainty of partner recognition is reduced since opponents are distinguished from non-opponents and aggressive displays are activated only in appropriate circumstances. A study on butterfly fish showed how the "tail up" display functioned in reducing the risk of failure in the recognition process of the conspecific encountered (Yabuta, 2002). In addition, recognition cues seem to be achieved through greeting displays in spotted hyenas, where the risk of a mistaken identity in the reunion context seems to be reduced through the mutual inspection of scents (East, et al., 1993). Furthermore, several species use vocal signals to either maintain contact when separated or vocalise prior to joining a new subgroup. For example, hyenas use vocal communication to maintain contact between clan mates in other subgroups (Theis, Greene, Benson-Amram & Holekamp, 2007). Chimpanzees are able to distinguish calls of community members from other neighbouring communities and from strangers (Herbinger, et al., 2009). The extent to which individuals are capable of identifying every group member during a fusion event is unknown, but it is very likely that vocal communication serves as a first communicative signal. In addition, there is evidence suggesting spider monkeys (*A. geoffroyi*) take into account individual variation in voice, at least for some familiar individuals (Teixidior & Byrne, 1999). If such vocalizations convey information at individual level, then recognition between two individuals at reunion might be resolved without the need of close approaches. This way the risk associated with

uncertainty related to recognition would be notably reduced in species that use vocal communication in the context of reunions.

A second function of affiliative interactions performed in reunion context is provided by the bond testing hypothesis (Zahavi, 1977). The authors suggest that social animals can obtain honest information about the quality of their dyadic relationships by exchanging costly high-risk signals. Relationships are likely subject to changes in time and temporal separation of two individuals might have created a "break" in the succession of interaction that defines the relationship (Hinde, 1976, see Chapter 1). In addition, when individuals are separated interactions with third parties may alter the dynamics of a given social relationship and affect the interests of one or both participants in maintaining the relationship. Therefore, after being temporarily separated individuals might need to ascertain the stability of the bond, or otherwise acknowledge a change in the relationship. The extent to which any individual submits itself to potentially high risk approaches and contacts with rejoining individuals, potentially conveys information about its commitment to the relationship (Zahavi, 1977). For example, in spotted hyenas the exposure of vulnerable parts of the body in the scent inspection display might not only help in the identification process (East et al., 1993), but it also conveys information about the commitment of the participants in maintaining or forming a relationship (Colmenares, et al., 2000). Male baboons (*P. hamadryas*) typically greet each other by touching or grasping the other's rear or penis, which is also a gesture of high risk exposure (Colmenares, et al., 2000). Furthermore, a study on Guinea baboons (*P. papio*) demonstrated how the use of intense greetings was directed to test the quality and strength of the partners' social relationship (Whitham & Maestripieri, 2003). Spatial and temporal separation might also affect individuals' relationships. Individuals might need to recover security about their relationships with individuals they have not been together with for a given period of time (Aureli, et al., 2008).

A third proposed function of greetings is to reassure individuals about the intentions of others in a reunion context. Fusion events refer to a specific type of reunion event that applies to species characterised by a high degree of fission-fusion dynamics (FF dynamics), in which individuals from the same community are rarely all together (Chapter 1), and is when individuals from different subgroups join

together to form a new subgroup. These events are potentially conflict-enhancing given the potential for increases in conflicts of interest that might arise from having a subgroup comprised of different individuals. Fusion events might also produce a sudden increase of competition among resources, which would serve to increase uncertainty among individuals. In fact, the number of individuals that can jointly feed without incurring intragroup feeding competition depends by the patch size and density of the food within it (Symington, 1988; Chapman, Wrangham & Chapman, 1995). Given that fission is hypothesized to reduce feeding competition by individuals splitting into smaller subgroups (Kummer, 1971), an increase in competition might be expressed in the aftermath of fusion, even if only for a short period of time. Therefore, it is reasonable to conclude that tension and the potential for aggression might increase when subgroups fuse together due to an increase in competition among subgroup members. The high frequency with which species living with high FF dynamics deal with fusion events may have favoured specific or more sophisticated signals compared to species living with a much lower degree of FF dynamics (Aureli, et al., 2008; Chapter 1). Individuals living in societies with a high FF dynamics would then use signals to cope with the tension associated with increased post-fusion competition, thus representing a mechanism to prevent escalation of aggression.

5.1.2 Aims of the study

Collectively, the need to recognise community members at fusion, to reaffirm bonds after a period of separation and to cope with increased competition within joining subgroups all likely contribute in making fusion events tension-ridden situations. The goal of my study was to investigate post- fusion behaviour in wild spider monkeys. The first aim was to test whether fusion events were responsible for an increase in tension and thus anxiety experienced by the individuals involved. The second aim focused on whether affiliative and aggressive behaviours were more likely to occur after fusion events and whether such behaviours were more common among individuals of joining subgroups. The third aim was to investigate whether components of relationship quality influenced either post-fusion affiliative or aggressive behaviours. Finally, the fourth aim was to examine whether post-fusion

affiliative behaviours functioned to reduce potential increases in post-fusion aggression and anxiety.

5.2 Methods

5.2.1 Subjects

Data were collected on all the adult and juvenile members of both sexes in the two communities (Chapter 2). Data were collected on an all occurrences or *ad libitum* basis on all individuals involved in fusion events and in friendly behaviours, respectively (Chapter 2).

5.2.2 Procedure

Fifteen minutes post-fusion focal observations were collected as soon as possible after a fusion event on one individual of the two joining subgroups. In order to obtain the most equal number of observations of all individuals, I gave priority to the individuals for which the smallest number of focal observations was available. For every post-fusion observation I extracted a MC from baseline focal observations, which were not preceded by a fusion event within the previous two hours, with the subgroup composition most similar to the corresponding post-fusion observation.

Fifteen minute post-embrace focal observations were collected as soon as possible on any individual engaged in a friendly behaviour (embraces, pectoral sniffs and kisses, Chapter 2, section 2.5). For every post-embrace focal I extracted a MC that was known not to be preceded by friendly behaviour for at least two hours. MC observations were extracted from focal observations with the subgroup composition most similar to the corresponding post-embrace focal, which had to include the individual who engaged in the friendly behaviour with the focal animal in the corresponding post-embrace focal. All occurrences of aggressive events and friendly behaviours were used to investigate their latency in post-fusion observations, post-embrace focals and their corresponding MCs.

To calculate post-fusion and post-embrace observation scratching rates I followed the same procedure as for post-conflict scratching rates (see Chapter 4, section 4.2.4). In addition, in post-embrace focals to control for an effect of proximity on scratching rates, I selected only MCs starting after an approach or proximity, the latter included all instances where individuals were at least within arm's reach or in contact. The duration of the controlled MCs was adjusted to the corresponding post-embrace focals in order to obtain post-embrace focal-MC pairs of the same duration.

In post-embrace focals, to control for an effect of approaches and proximity on the proportions of proximity, I selected only MCs starting after an approach or proximity. The duration of every MC was then adjusted to the corresponding post-embrace focal to obtain post-embrace focal-MC pairs of the same duration. Proportions of instantaneous scans in contact and proximity were obtained by dividing the total number of scans in contact or proximity by the total number of scans in each post-embrace focal and MC.

5.2.3 Statistical Analyses

To examine whether fusion events led to anxiety I compared scratching rates of post-fusion observations and corresponding MCs with paired-sample t-tests. The test was run for the whole duration of post-fusion observations and MCs and for only the first five minutes. I also tested for a difference in scratching rate on post-fusion observations where no friendly behaviour occurred within the first five minutes to control for a possible effect of friendly behaviour on scratching rate.

I analysed whether in the aftermath of a fusion event individuals were more likely to be involved in aggressive behaviour compared to MCs following de Waal and Yoshihara's (1983) PC-MC method. For all post-fusion-MC analyses, in cases where the measures did not violate the assumption of normality (Siegel & Castellan, 1992), analyses were performed with paired t-tests, whereas when the assumption of normality was violated comparisons were performed with a Wilcoxon sign rank test. Post-fusion -MC pairs were labelled "early" if the focal individual was involved in aggressive behaviours earlier in the post-fusion observation than in the MC. If aggressive behaviours occurred earlier in the MC the pair was labelled "late".

Proportions of early and late pairs were calculated at the individual level for post-fusion observations and MCs with the Wilcoxon signed rank tests. Since all comparisons involved Ns < 15, the T and corresponding exact p values are reported (Siegel & Castellan, 1988). To investigate an effect of the role of the individuals engaging in friendly behaviours, the analyses were conducted at three levels:1) aggressive behaviours between the focal individual and any other individual; 2) between the focal individual and one individual of the joining subgroup; 3) the focal individual and one individual of the same subgroup, i.e., "non-joining individuals".

To determine the occurrence of aggressive behaviours over the total length of every daily observation, including censored observation (post-fusions and MCs where the observation ended before the occurrence of an aggressive behaviour), I performed a Kaplan-Meier survival analysis with a Mantel-Cox test at the individual level on the latency of aggressive behaviour from a fusion event (Chan, 2004). I compared latencies of aggressive behaviour for post-fusion observations with latencies of aggressive behaviour for MCs. When latencies were significantly different I identified a time window during which aggressive behaviour was most likely to occur. To determine whether fusion events had an effect on the occurrence of friendly behaviour and were more likely to occur in a specific time window, I followed the same procedure as for post-fusion aggressive behaviours.

Similar to the analyses I performed for post-conflict fission (Chapter 4, section 4.2.4), a linear mixed model (LMM) approach was applied to examine the effect of relationship characteristics, including kinship, sex composition of dyad, Compatibility and Risk (Chapter 3) on the latency of aggressive and friendly behaviour in the aftermath of a fusion. The relationship characteristics of every dyad of individuals were implemented with each dyad's latency of aggressive or friendly behaviour. Post-fusion observations with censored observations before the time window identified in the survival analysis were excluded from this analysis. Post-fusions where aggressive or friendly behaviour occurred after the defined time window were all considered as if the friendly behaviour occurred at the defined time window. In addition, to determine if friendly behaviour had an effect on the likelihood of aggressive behaviour in the post-fusion observations I used a Mann-Whitney test to compare whether aggression occurred between post-fusion

observations with friendly behaviour during the first minute and post-fusion observation where no friendly behaviour occurred in the first minute.

Post-embrace observations were employed to examine whether behaviour changed in the aftermath of friendly behaviour. To examine the changes in scratching, contact and proximity in the aftermath of a friendly behaviour, I applied de Waal and Yoshihara's (1983) PC-MC method following the same procedure for post-fusion scratching, contact and proximity. To control for an effect of proximity on scratching rates, I selected only MCs starting after an approach, a contact or proximity. In addition, I investigated whether the occurrence of aggressive events were influenced by friendly behaviour. A critical value of 0.05 was adopted as significant level for all tests and when appropriate a Bonferonni's correction was applied.

5.3 Results

5.3.1 Post-fusion scratching

I collected 87 post-fusion -MC pairs on 26 individuals (67 in the Eastern community and 20 in the western community). To investigate whether fusion events led to anxiety, I tested for differences in scratching rate in post-fusion observations and MCs. I found no difference in scratching rate during the entire 15 minutes of the post-fusion observations and the entire 15 minutes of the MCs [$t(23)=-.85$, $p=.40$, Table 5.1]. In addition, I did not find any significant difference in scratching rate when I compared only the first five minutes of the post-fusion observation s with scratching rate in the entire 15 minutes of the MCs [$t(23)=-.74$, $p=.47$, Table 5.1]. To control for a possible effect of friendly behaviours on anxiety I performed the same test on only post-fusion observations where no friendly behaviour occurred during the first five minutes. I found no difference in scratching rate during the first five minutes of the post-fusion observations with no friendly behaviour compared to the corresponding MCs [$t(21)=-1.47$, $p=.16$, Table 5.1].

Table 5.1 Mean ± S.E. of scratching rates for different intervals of post-fusion observations and relative MCs.

Post fusion duration	post fusion	MCs
15 minutes	.0047±.00043	.0054±.00058
5 minutes	.0047±.00057	.0054±.00058
5 minutes (no friendly)[1]	.0043±.00065	.0057±.00054

[1]=only post-fusion observations where no friendly behaviour occurred within the first five minutes

5.3.2 Post-fusion aggression

I found a significantly higher proportion of early than late pairs for aggressive events between the focal individual and any other individual involved in a fusion (Wilcoxon signed rank test: ties=16, n=10, T=2.5, p=.008, Figure 5.1), indicating that aggressive events were more likely to occur after a fusion event compared to MCs. Aggressive events with joining individuals occurred significantly sooner following a fusion compared to MCs (ties=18, n=8, T=2.5, p=.031; Figure 5.6), whereas there was no significant difference for aggressive events with non-joining individuals (ties=22, n=4, T=3.5, p=.750, Figure 5.1). Therefore, aggressive encounters were more likely to occur during the aftermath of a fusion and between joiners.

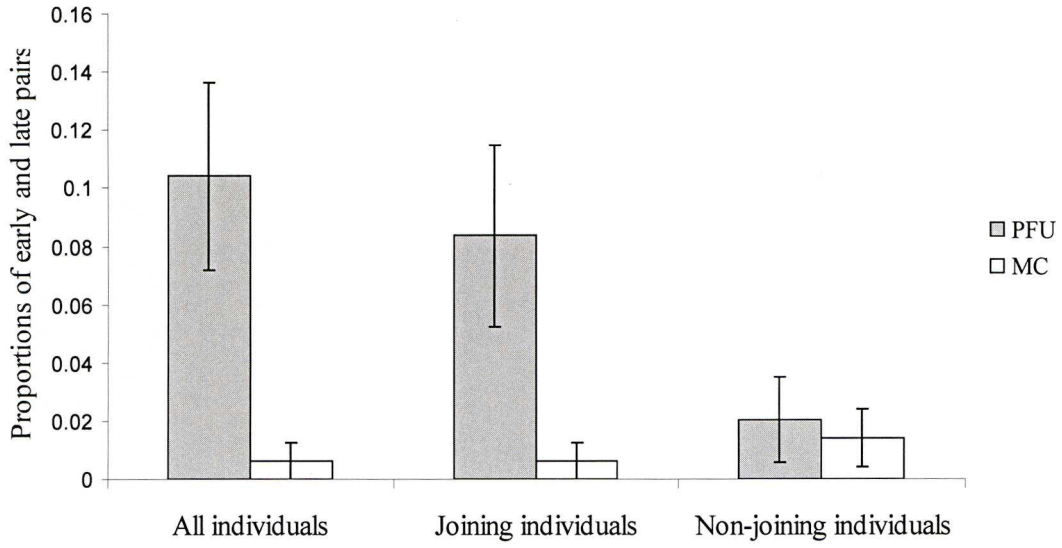

Figure 5.1 Mean (±SE) of proportions of early and late pairs of aggressive events in post-fusion observations (PFU) and MCs between the focal individual and all other individuals, only joining individuals and only non-joining individuals. * = significant difference between post-fusion observations and corresponding MCs.

I performed a survival analysis to test for difference in aggression latency in post-fusion observations compared to MCs at focal individual level. The latency to aggressive events with any other individual in the post-fusion observations was shorter compared to the MC [N=87, χ^2= 4.51, df=1, p=.034, Figure 5.2]. When I performed the analysis on aggressive events only with joining individuals, I found a tendency for a shorter latency in post-fusion observations compared to MCs (χ^2= 3.59, df=1, p=.058; Figure 5.3), whereas I found no significant difference with only non-joining individuals [χ^2=.89, df=1, p=.35, Figure 5.4]. The difference in latency to aggressive events was identified in a 3600 seconds time window.

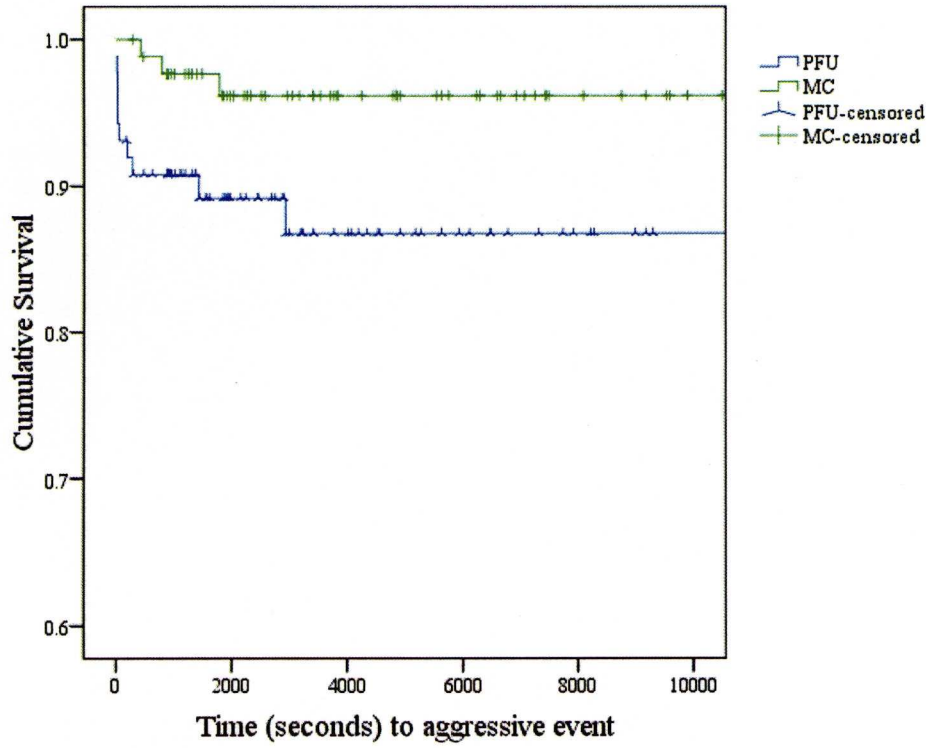

Figure 5.2 Latency of aggressive behaviours in post-fusion observations (PFU) and MCs between the focal individual and any other individual involved in the fusion event.

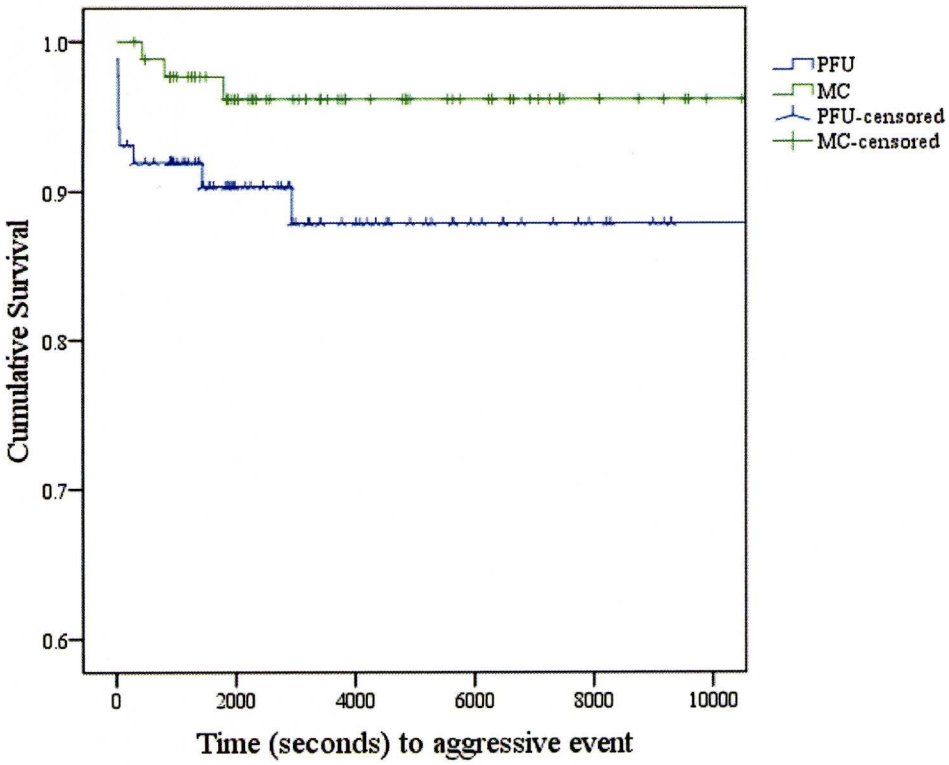

Figure 5.3 Latency to aggressive events between joining individuals in post-fusion observations (PFU) and MCs.

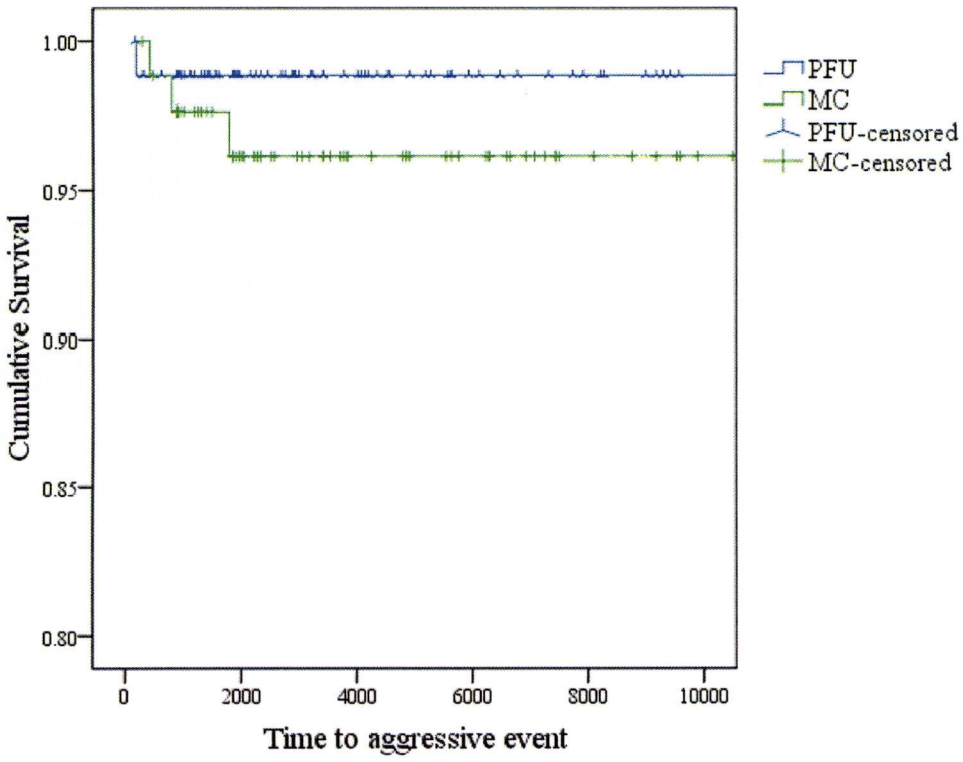

Figure 5.4 Latency to aggressive event between only non-joiners in post-fusion observations (PFU) and MCs.

5.3.3 Post-fusion friendly behaviours

Among all the individuals involved in a fusion event I found a significant difference in the proportion of early pairs and late pairs (Wilcoxon signed rank test: ties=14, n=12, T=0, p<.001, Figure 5.5). The result was due to the friendly behaviour between individuals from joining subgroups. There was a higher proportion of early than late pairs when I limited the analysis to friendly behaviours involving the focal individual and members of the joining subgroup (ties=15, n=11, T=0, p=.001, Figure 5.5). For individuals who were in the same subgroup before fusion events, proportions of early and late pairs were not significantly different as there were 24 ties between the early and late pairs, 23 of which had no friendly behaviour occurring during the time window (ties=24, n=2, T=0, p=.5, Figure 5.5). Therefore, friendly behaviours were more likely to occur following a fusion between individuals of joining subgroups.

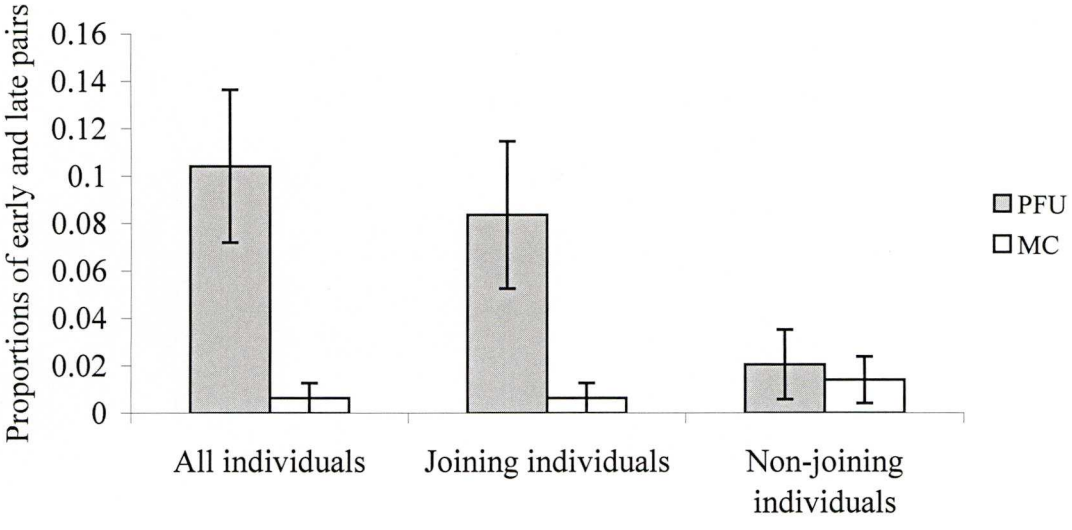

Figure 5.5 Mean (±SE) of proportions of early and late pairs of friendly behaviours in post-fusion observations (PFU) and MCs between all individuals, between joining individuals and between non-joining individuals. * = significant difference between post-fusion observations and corresponding MCs.

Next, I conducted a survival analysis to test the difference in latency of friendly behaviours in post-fusion observations compared to MCs. Friendly behaviours occurred significantly earlier in post-fusion observations compared to MCs (Mantel-Cox: N=87, χ^2= 12.55, df=1, p<.001; Figure 5.6), and among only joining individuals (χ^2= 9.27, df=1, p=.002, Figure 5.7). When I tested only non-joining individuals there was no significant difference in the latency to friendly behaviour (χ^2= .000, df=1, p=.986). The difference in latencies to friendly behaviour in post-fusion observations and MCs was identified in a time window of 300 seconds.

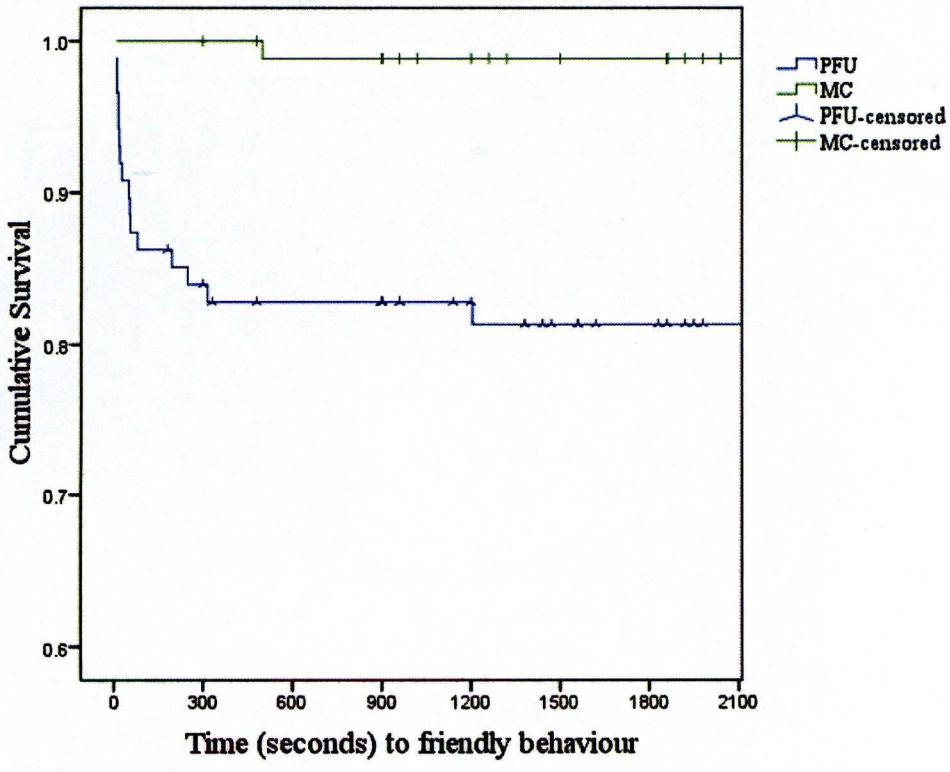

Figure 5.6 Latency of friendly behaviours in post-fusion (PFU) observations and MCs between the focal individual and any other individual involved in the fusion event.

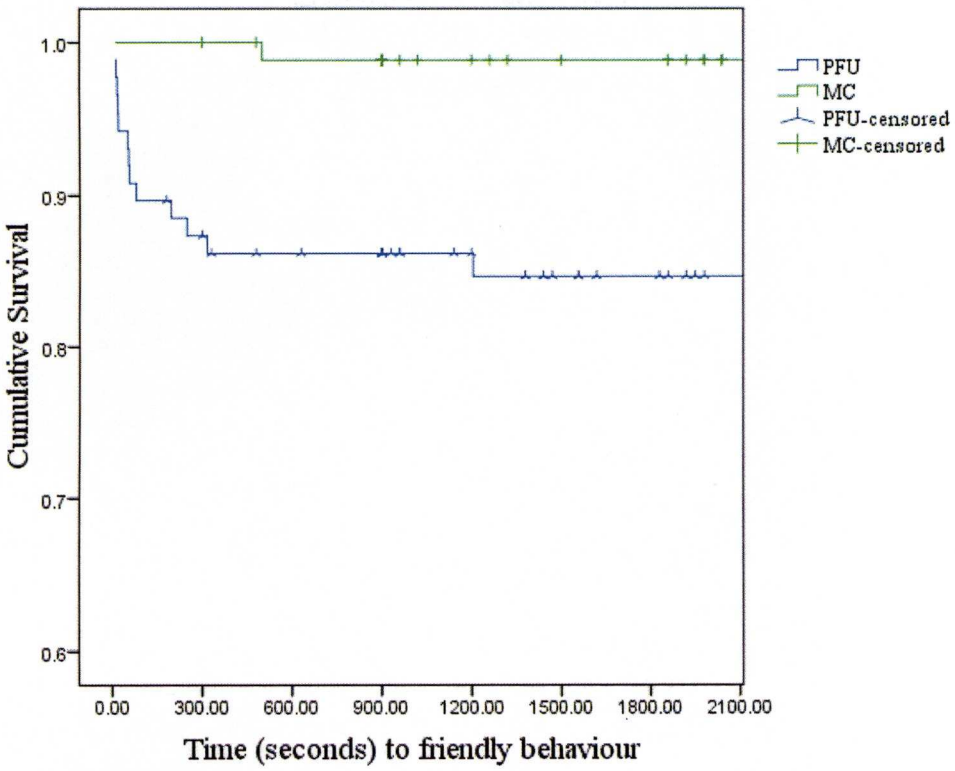

Figure 5.7 Latency of friendly behaviours in post-fusion observations (PFU) and MCs between the focal individual and joining individuals.

To test the role of friendly behaviours in post-fusion observations, I compared the proportion of aggression within the first five minutes in post-fusion observations after an embrace during the first minute (N=10) and the proportion of aggression in post-fusion observations where no embrace occurred during the first minute (N=24). In the aftermath of a fusion the occurrence of aggressive events was less likely if preceded by a friendly behaviour in the minute following the fusion [Mann-Whitney test: N_1=10, N_2=24, U=80.00, Z=-2.03, p=.042: post-fusion observations (with embrace)=.00 ± .00; post-fusion observations (without embrace) =.13±.05].

5.3.4 Post-fusion behaviour and relationship characteristics

I performed a LMM to test whether the latencies to friendly behaviours following a fusion were affected by the characteristics of the relationship between the individuals involved (Table 5.2). The best model explaining the latency of friendly behaviours included only Risk (Table 5.3). Risk had a significant negative effect on latency to friendly behaviour suggesting that individuals with riskier

relationships were involved in friendly behaviours significantly sooner compared to non-risky partners.

Table 5.2 Predictors used for LMM on the influence of relationship characteristics on postfusion latency to friendly behaviour.

Fixed factor	Sex, age, kinship, tenure, compatibility and risk
Random factor	-
Dependent factor	Post-fusion latency to friendly behaviour

Table 5.3 Results of the best LMM indicating the influence of relationship characteristics on post-fusion latency to friendly behaviour.

Independent variable	β	SE	t value	p value	95% low and high confidence intervals
Risk	-23.17	3.60	-6.44	<.001	-31.5--14.78

Only variables present in the best model are shown.

The best model explaining the latency to aggressive behaviours included subgroup membership, risk, compatibility, kin and sex (Table 5.4 and 5.5). Risk and kinship had a significant and negative effect on latency to aggressive behaviours. Individuals with riskier relationship engaged in aggressive behaviour sooner than individuals with less risky relationships. The results obtained on kinship indicate that non-kin have longer latencies to aggression compared to kin, but this finding is an artefact as only 10 of the 54 kin dyads engaged in aggressive behaviour at all (latencies to aggressive behaviour mean ±SE, kin: N=54; 300.00±0.00; non-kin: N= 433; 294.0416±1.90226). Compatibility had a significant positive effect on latency to aggression indicating that more compatible dyads tend to engage in aggression later compared to less compatible dyads. The effect of the composition of sex dyads resulted in male-male dyads with significantly shorter latencies to aggression compared to the other sex combinations.

Table 5.4 Predictors used for LMM on the influence of relationship characteristics on post-fusion latency to aggressive behaviour.

Fixed factor	Sex, age, kinship, tenure, compatibility and risk
Random factor	-
Dependent factor	Post-fusion latency to aggressive behaviour

Table 5.5 Results of the best LMM indicating the influence of relationship characteristics on post-fusion latency to aggressive behaviour.

Independent variable	β	SE	t value	p value	95% low and high confidence intervals
Risk	-24.83	3.02	-8.21	<.001	-30.78- 18.89
Compatibility	5.91	2.23	2.65	0.008	1.53-10.29
Kinship	-21.16	6.29	-3.36	0.001	-33.52-8.79
Sex (FF-MM)	18.20	7.49	2.43	0.026	2.40-34.01
Sex (FM-MM)	11.85	5.70	2.08	0.041	.51-23.20

5.3.5 Post-friendly behaviour and scratching

I collected 49 post-embrace observation-MC pairs on 19 individuals (six in the Western group and 43 in the Eastern group). I investigated whether the exchange of friendly behaviours had an effect on anxiety comparing the scratching rates of the post-embrace observations with the scratching rates of MCs. I found no difference in scratching rates over the entire 15 minutes of post-embrace observations and during the first five minutes of the post-embrace observations compared with the entire 15 minutes of the MCs [entire 15 minute: $t(18)=.368$, $p=.717$; first five minutes: $t(18)=.436$, $p=.668$; Table 5.6]. Then, I extracted 15 MCs (on 12 individuals) starting after an approach or contact or proximity and matched them with the corresponding post-embrace observations to control for the possibility effect of proximity that is always the case in post-embrace observations. The scratching rate of the first five minutes of post-embrace observations compared to MCs following an approach or a contact/proximity was not significantly different [$t(11)=-1.27$, $p=.23$; Table 5.6].

Table 5.6 Mean±SE of scratching rates of post-embrace observations and MCs during the first 15 minutes and the first five minutes, and during the first 5 minutes of post-embrace observations matched with MCs controlled for approach, contact and proximity.

	Post-embrace observations	MCs
15 minutes	.005±.0007	.0050±.0006
First 5 minutes	.006±.0008	.0050±.0006
First 5 minutes (controlled)[1]	.002±.0014	.005±.001

[1]= Post-embrace observation-MC pairs controlled for approach, contact and proximity

5.3.6 Post-embrace behaviour contact and proximity

The proportion of scans in contact and proximity was higher in post-embrace observations compared to MCs [$t(18)=2.61$, $p=.018$]. When I limited the analysis to MCs starting from either an approach of the partner or a contact or proximity with the same individual engaging in friendly behaviour in the corresponding post-embrace observation, I found that the proportion of scans in contact and proximity was higher in the MCs compared to the post-embrace observations [$t(11)=-2.875$, $p=.015$].

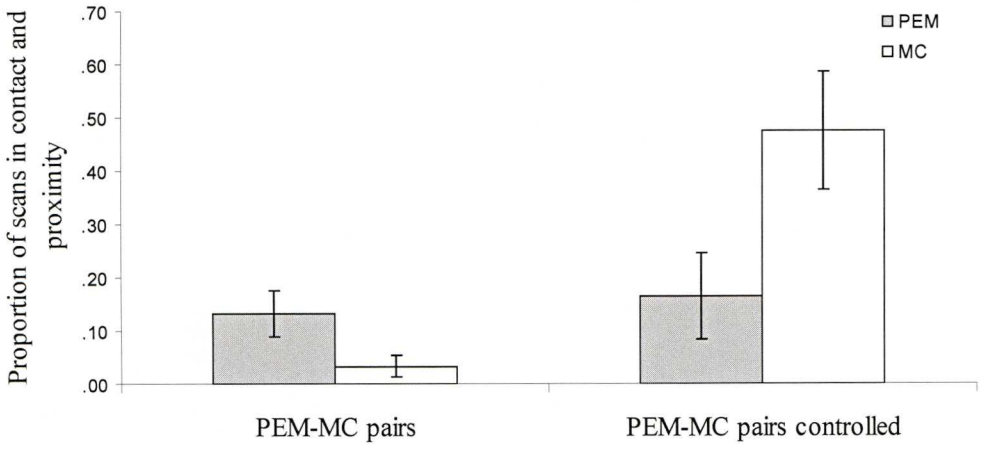

Figure 5.10 Mean (±SE) proportions of scans in contact and proximity in all post-embrace observation-MC pairs and in post-embrace observation (PEM) -MC pairs controlled for an effect of approach, contact and proximity. * = significant difference between post-embrace observations (PEM) and corresponding MCs.

5.4 Discussion

My first aim was to test whether fusion events were responsible for an increase in tension and thus anxiety experienced by individuals at fusion. I found no evidence that scratching rates increased following fusion. My second aim focused on whether affiliative and aggressive behaviours were more likely to occur after fusion events and whether such behaviours were more common among individuals of joining subgroups. I found that aggression and friendly behaviour were more likely at fusion among joining individuals and both behaviours were more frequent during the first five minutes following a fusion event. My third aim was to investigate whether components of relationship quality influenced post-fusion affiliative or aggressive

behaviours and I found that dyads with risky relationships were more likely to engage in friendly and aggressive behaviour sooner than dyads with less risky relationships. Kin related individuals had shorter latencies to aggression compared to non-kin. Furthermore, compatibility had a significant effect on latency to aggressive behaviour suggesting that individuals with compatible relationship engage in aggressive behaviour later than less compatible dyads. The effect of composition of sex dyads showed that male-male dyads engage significantly sooner in aggressive displays after a fusion compared to the other sex combination dyads. My fourth aim was to examine whether post-fusion affiliative behaviours functioned to reduce a potential increase in post-fusion aggression and anxiety. I found support for a reduction in post-fusion aggression, but no evidence for a reduction in anxiety as measured by scratching behaviour.

5.4.1 Post-conflict anxiety

One explanation why I did not find evidence of post-fusion anxiety might lay in the temporal delay of post-fusion observations in respect of the peak of anxiety. It is likely that individuals who are about to join another subgroup are aware of the forthcoming fusion event before the observer started a post-fusion observations and by the time my observations began I may have missed the critical time window for an increase in scratching. Individuals were not considered belonging to the same subgroup if the closest distance between two individuals of different subgroups was more than 30 meters. Therefore, in my study post-fusion focal observation were started when individuals of joining subgroups were already relatively close and it is possible members of both subgroups could have seen each other before I was aware a fusion was underway. In addition, it is possible that through vocal communication individuals are alerted and informed about a possible fusion event and there is some evidence suggesting that whinny calls serve this function in spider monkeys (van Roosemalen & Klein, 1988; Ramos-Fernández, 2005). My study however did not incorporate scoring whinny vocalisations in the context of fusion and is an area of further investigation. Furthermore, scratching reflects short term anxiety and in various primate species scratching rates due to post-conflict anxiety reached a peak during the first minutes after a conflict and then gradually dropped down to baseline (Japanese macaques, *Macaca fuscata* :Schino, et al., 2007; Kutsukake & Castles

2001; long tailed macaques, *M. fascicularis* : Das, et al., 1998; chimpanzees: Koski, Koops & Sterck, 2007). Given that scratching is found to drop after the first few minutes from the critical event, it is possible that such a measure of anxiety was not captured in my post-fusion observations.

5.4.2 Aggression and friendly behaviour at fusion

Aggressive events were more likely to occur after a fusion event. Aggressive events occurred significantly sooner compared to MCs among individuals of joining subgroups. These results are in line with a recent study on post-fusion aggression in spider monkeys conducted on the same communities (Aureli & Schaffner, 2007) and confirm that fusion events bear a high potential for aggression, especially between individuals who encounter each other after a temporal separation. However, in my study a time window of one hour was identified for latencies to aggression to match baseline levels. This indicates that the potential for aggression is still high in the hour following a fusion event although the strongest increase in aggression occurs in the immediate aftermath of a fusion event. The reason underlying the occurrence of such aggressive displays is likely related to the increased intragroup competition among feeding resources (Symington, 1988). Thus, in this case aggressive displays are expected to be higher when the fusion occurs in a feeding context or in highly valuable food spots. In that case aggressive displays might function in establishing a feeding priority of the displayer over other individuals. However, this hypothesis is in contrast with the selective occurrence of aggressive behaviours between individuals of the two joining subgroups. In fact, feeding competition should involve all the individuals meeting at a given food spot, with no distinction between individuals who just encountered and individuals who were already together. Unless feeding competition is expressed at "subgroup level". For example, one interpretation is that individuals range in subgroups to avoid feeding competition, but when subgroups come together to a special feeding spot, as a rich fruiting tree, then scramble competition can arise, where individuals of one subgroup attempt to displace individuals of the encountered subgroup from the feeding resource. This would mean that competition over resources occurs also at a temporal level, where individuals who access first a valuable feeding spot gain the highest food intake. It could be assumed that further aggressive episodes are likely to occur until the food patch is

completely depleted, which might account for the time window of an hour found for aggressive displays after fusion events. In other contexts, apart from feeding, aggressive displays at fusion might be due to the competition of males over females. In that case conflicts among males should be higher compared to other sex combinations (see below). The selective occurrence of aggressive behaviours between individuals of the two joining subgroups is unclear.

Friendly behaviours (embraces, kisses and pectoral sniffs) increased in the post-fusion context relative the MCs. In addition, the time window for embraces was within five minutes from a fusion event compared to MCs. My findings replicate those reported earlier for captive and wild spider monkeys (Schaffner & Aureli, 2005; Aureli & Schaffner, 2007). However, my analyses have gone further to examine the characteristics of individuals that exchange the friendly behaviour in the post fusion context (see below). Given the time window of five minutes and that the embraces, kisses and pectoral sniffs are selective between individuals that are joining together suggests the behaviours functions as greetings.

Greeting behaviours might function to provide individuals with "assessment time" to recognise each other after a temporal separation (Yabuta, 2008). In spider monkeys however individual recognition is likely accomplished through other behaviours that do not entail physical contact. Vocal communication might function in individual recognition (Teixidior & Byrne, 1999; Ramos-Fernández, 2005). Spider monkeys' whinnies are a means by which individuals can identify other group members when they are far apart from each other. Furthermore, it is likely that individual recognition might also be achieved visually. Face greetings are also exchanged at a variable distance and are directed towards specific individuals (Eisenberg, 1976; Teixidor & Byrne, 1999) possibly reflecting some degree of individual recognition. Therefore, in most cases individual recognition is likely to be achieved prior to engaging in friendly behaviours. Thus, in spider monkeys greeting gestures are probably not usually associated with individual recognition.

Greeting gestures may also provide animals with information about their relationship such as the partners' commitment to maintain the relationship after a temporal separation (Zahavi, 1977). Due to their high degree of fission-fusion (Symington, 1990; Chapman, et al., 1995) spider monkeys regularly encounter other

group members after a temporal separation. Thus individuals frequently face the uncertainty related to the relationship shared with an encountered group member so that greeting gestures might have evolved as a means to communicate the partners' interest in its maintenance. Zahavi (1977) proposed that honest communication is preserved when signals are risky to give or when signals are very costly. In species with a high FF dynamics proximity in the context of a fusion event can be very risky given the high potential for aggression between joiners (chimpanzees; Bauer, 1979; Goodall, 1986; spider monkeys: Aureli & Schaffner, 2007). Furthermore, the exposure of vulnerable parts to the partner's jaw during an embrace or a pectoral sniff is a risky undertaking that might add reliability and reduce the likelihood of deceit. However, if the underlying function of embraces at fusion events is to test the relationship, than greeting gestures should be proportionally related to the length of time two individuals were apart. As relationships are in part defined by interactions between two individuals over time (Hinde, 1976), after a temporal separation individuals might need to reaffirm their interest in the relationship. It could be predicted that the longer two individuals were apart the more likely it is that their commitment in the relationship was subject to some change. However, my research methodology did not allow me to quantify the time two individuals were apart as it is an exceptionally difficult undertaking in communities characterised by high FF dynamics. Thus, I was not able to test that hypothesis, but it is certainly worth addressing this question in future studies.

It is also possible that embraces during fusion events function to communicate peaceful intentions and reduce the risk of aggression. In circumstances of uncertainty it may be very costly to be in close proximity with individuals with whom potential for aggression is high. In such circumstances it pays to signal benign intention to avoid the potential for aggression (Silk, 2002). Some primates use quiet calls to communicate their peaceful intentions (Silk, 2002). In female rhesus macaques approaches to other females are frequently followed by aggression. However, the emission of grunts or girneys during an approach significantly reduced the likelihood that aggression would occur. Thus, females communicate their good intentions via vocalization (Silk, Kaldor & Boyd, 2000). In species with high FF dynamics, fusion events are associated with high potential for aggression as shown in this study and others (Bauer, 1979; Aureli & Schaffner, 2007). It seems reasonable therefore that

behavioural displays to reduce tension and promote tolerance may have evolved to cope with frequent fusion episodes. Aureli and Schaffner (2007) suggested that embraces and pectoral sniffs at fusion events might be effective in appeasing and reassuring other individuals given the rapid modality in which the message is conveyed. Thus, greeting gestures might serve the function to signal peaceful intention and restore tolerance levels during fusion events in spider monkeys. In my study friendly behaviours were more likely exchanged between individuals of joining subgroups, which relates to the benign intent hypothesis of Silk (2002) because aggressive behaviours are more common between joining individuals at fusions. The communication of benign intentions is important for those individuals with whom aggressive interactions is more likely and it was those individuals, whose relationships were characterised by high risk which exchanged embraces sooner after fusion (see below). Furthermore, the function of embraces as good intention signals is confirmed by the fact that I demonstrated that embraces not only reduced the likelihood of aggression, but were absent from fusion events in which the exchange of friendly behaviour occurred soon after fusion between individuals from joining subgroups.

5.4.3 Components of social relationships and post-fusion behaviour

The function of friendly and aggressive behaviour during fusion events could best be interpreted in light of the result of the effect of relationship quality on latency to friendly and aggressive behaviour. In my study individuals with riskier relationships were involved in friendly and aggressive behaviours significantly sooner compared to non-risky partners. Furthermore, dyads with more compatible relationships engaged in aggressive displays later than dyads with less compatible relationships. These results suggest that the most important function of affiliative behaviours is to prevent aggressive interactions. Individuals sharing risky relationship are more subject to be involved in aggressive encounters compared to individuals with less risky relationships and are therefore more motivated to engage in friendly interaction to avoid aggression. The high potential of aggressive interaction in individuals with risky relationships may induce them to communicate their peaceful intentions before aggression escalates. It seems that the temporal pattern of such friendly behaviour is crucial during fusion events, where delayed friendly behaviour

intent might be costly as aggressive behaviour is more likely to take place. This critical timing in behavioural communication of intention may explain the short time window found for the latency to friendly behaviours following a fusion event. In addition, the shorter latencies to both friendly and aggressive interactions for individuals with riskier relationships demonstrate the causal connection of those two behaviours. If no prior peaceful intentions are communicated, then individuals with riskier relationships are likely involved in aggressive displays. Indeed when interactions involve high risk, communication of intention should occur before any other interaction (van Schaik & Aureli, 2000). Individuals might want to interact with the encountered group members to reassess the state of their relationship or to simply access feeding resources but need to communicate their good intention prior to any other interaction.

Dyads with more compatible relationships, instead, engaged in aggressive displays significantly later compared to less compatible dyads. The general tenor of tolerance that characterises Compatibility (Cords & Aureli, 2000; Fraser, et al., 2008) may explain why aggressive events occur with longer latencies among more compatible dyads compared to less compatible dyads. In addition, male-male dyads had shorter latencies to aggression after fusion compared to other sex combinations, although no significant results were found for friendly behaviours to be associated with a specific sex dyad composition. If embraces serve the function to prevent aggression, then such behaviour should also be higher between males, and van Roosmalen and Klein (1988) report that in the reunion context embraces and pectoral sniffs were more frequent between males compared to females. It may be possible that I did not have a sufficient number of cases to detect such differences as my sample size was relatively small for embraces. That male dyads had a shorter latency to aggression than either male-female or female dyads indicates that sexual competition could be responsible for aggression at fusion, as males are more likely to compete over mates than over food (Clutton-Brock & Parker, 1992). The sudden increase in the number of individuals that characterises a fusion event could create aggressive arousal not only over food, a classic source of competition for females, but also for reproductive females. In that case I would not expect to see aggression at fusions if no reproductive females are involved. Thus, in future studies, it would be

interesting to investigate whether the occurrence of aggression is related to the type and composition of encountering subgroups.

Collectively, my results best support a benign intent perspective. It is possible that bond testing is a further function of embraces at fusion, although it could not be verified in my study given the absence of a component of relationship quality that corresponds to Value. Indeed, I would have expected greeting behaviours to have shorter latencies in individuals with more valuable relationships. However the absence of this component in my study does not permit a full investigation of that possibility.

5.4.4 Post-embrace scratching and proximity

Only a few studies have examined the function of embraces on anxiety in spider monkeys. In addition, embraces in spider monkeys are associated with fusion events and may best function to signal benign intent and in turn reduce tension (Schaffner & Aureli, 2005; Aureli & Schaffner, 2007; Rebecchini, this study). Embraces were also found to be related with the feeding context in captive spider monkeys (Pastor-Nieto, 2001). The function of benign intent provided by embraces was also suggested in the context of tolerance around infants (Schaffner & Aureli, 2005). However, more recently a study on wild spider monkeys reported evidence for embraces to be exchanged in a biological market for infant handling (Slater, et al., 2007). It would have been a strong piece of evidence if I was able to demonstrate that embraces have an appeasement effect by reducing scratching rates of either the performer or recipient of embraces. The scratching rate of individuals who just engaged in a friendly behaviour, however, was not significantly lower compared to MCs. The result did not change when it was controlled for approaches or contact/proximity. This could be explained in one of two ways. Firstly, small sample sizes may mean I did not have sufficient statistical power to find an appeasement effect on anxiety levels determined through scratching rates. Secondly, there may have been a problem with the protocol I used. I compared scratching between post-embrace observations and MCs, but a more sensitive measure might have been to examine the effect of friendly behaviours on scratching rate by comparing immediate pre and post friendly scratching rates. In fact, the effect of friendly behaviours on scratching rates is likely to bring the levels of anxiety quickly back to a baseline

measure. Instead, the period preceding a friendly behaviour could be experienced as highly tense, which is why embraces are performed.

No evidence was found for increased contact and proximity between individuals who just engaged in friendly behaviours. The higher proportions of proximity and contact found after friendly behaviours may have been due to an effect of approaches, contact and proximity. In fact, proportions of contact/proximity were higher after approaches or contact/ proximity, compared to individuals who engaged in friendly behaviours. Individuals who are already in contact or in proximity are likely to keep that closeness for a while, as those behaviours are frequently associated with resting behaviour that lasts for extended time periods in spider monkeys (Di Fiore & Campbell, 2007). Thus, the best control would be to use only approaches and compare proportions of contact/proximity after friendly behaviours with proportions of contact/proximity after approaches. However, this comparison was not possible given the small number of approaches not followed by friendly behaviours and involving the same individuals engaged in friendly behaviour of the corresponding post-embrace observation.

5.4.5 Conclusions

Friendly behaviours were demonstrated to reduce the likelihood of aggressive interactions. Although my study, in part, replicates the findings of Aureli and Schaffner (2007) it also demonstrates for the first time that the risk entailed in fusion events can weigh differently according to the component of relationship that define joining individuals. The analyses of how components of relationships affect latencies of friendly and aggressive behaviour after a fusion contributed to identifying the function of friendly and aggressive behaviour in such critical contexts. Individuals with riskier relationship engaged sooner in friendly and aggressive behaviours at fusions underling how crucially important it is in risky relationships to communicate good intentions to prevent the escalation of aggression. The effect obtained for risky relationship on latency to friendly behaviours might also explain the selectivity of aggressive displays in the fusion context. In fact, the association pattern was included in the component of a relationship that defines compatibility, not risk (Chapter 3). Indeed, dyads defined by high compatibility experienced longer latencies to aggression compared to less compatible dyads. Thus, this independence of sub-

grouping from risky relationships might explain why at fusions aggressive displays occur primarily between joining individuals. Furthermore, male-male dyads shared more risky relationships compared to other sex combinations and indeed were involved in aggressive displays sooner than other sex combinations (Chapter 3). Thus, this result might indicate that aggressive displays between males at fusion could be due to sexual competition. Furthermore, a study of the context of fusion events might provide relevant elements to examine the underlying factors of aggressive and friendly behaviours at fusion events. Finally, the function of friendly behaviour on anxiety levels and contact or proximity, should be performed on a wider dataset to obtain meaningful results. The size of my dataset was very likely undermined by the advent of two hurricanes, which had dramatic effects on the subgrouping dynamics of the spider monkeys during my data collection.

Chapter 6

The impact of hurricanes on activity budgets and subgrouping dynamics.

6.1. Effects of hurricanes on natural environments

Hurricanes and typhoons are particularly intense tropical cyclonic storms that in more mild forms are referred to as cyclones or tropical storms (Lugo, Roger & Nixon, 2000). Hurricanes typically form over the ocean surfaces as a result of the conjunction of specific physical factors, such as ocean surface temperature and increasing humidity (Hoyos, Agudelo, Webster & Curry, 2006). Hurricanes are rated according to the Saffir/Simpson scale and are determined by maximum wind speed, atmospheric pressure and storm surge (see Table 6.1, Lugo, 2000).

Global warming is thought to have an effect on tropical climatic activities. Indeed, there is evidence that ocean surface temperature increased by roughly 0.5°C between 1970 and 2004 in tropical regions (Webster, Holland, Curry & Chang, 2005; Trenberth, 2005) and a 0.5°C increase in surface water temperature in the Gulf of Mexico played a key role in the increased hurricane activity in 2005 (Saunders & Lea, 2008). These climatic changes will likely affect the intensity of hurricanes and the overall volume of rainfall in the coming years, but how they will affect total hurricane numbers is unclear. There is a trend of increasing category 4 and 5 hurricanes from 1970 to 2004, which has been associated with increases in sea-surface temperature (Hoyos et al., 2006), and sea-surface temperatures in the Gulf of Mexico are projected to increase in the coming years, which may lead to a 40% increase in hurricane activity (Saunders & Lea, 2008). Furthermore, during the second half of the past century seven hurricanes of category 5 reached the Gulf of Mexico and Caribbean coasts (Jauregui, 2003), whereas between 2000 and 2007, eight category 5 hurricanes formed in the same area of the western Atlantic ocean (Blacke, Rappaport & Landsea, 2007; National Hurricane Center, 2010).

Table 6.1 Saffir/Simpson hurricane scale.[1]

Saffir/Simpson rank	Atmospheric pressure of storm centre (mbar)	Maximum sustained wind speed (km/h)	Storm surge (in metres)
1	980	119-153	1.0-1.7
2	965-979	154-177	1.8-2.6
3	945-964	178-209	2.7-3.8
4	920-944	210-249	3.9-5.6
5	<920	>249	>5.6

[1] Adapted from Lugo (2000)

The effects of hurricanes on the ecosystem can be dramatic and have been documented in various studies. The extremely strong winds can affect the microenvironment of forests in terms of light, temperature and humidity profiles due to a reduction in canopy cover (Lugo et al., 2000). The most common damage to forest structure, brought about by intense windstorms that accompany hurricanes, are the defoliation of trees, the loss of small and large branches, and, least common, the snapping and uprooting of tree trunks (Dittus, 1985; Brokaw & Walker, 1991; Pavelka, Brusselers, Nowak & Behie, 2003; Bonilla-Moheno, under review). Consequently, fruits, flowers and leaves are scarce in the immediate period following a hurricane. For example, in the aftermath of category 4 Hurricane Georges, which hit the Caribbean in 1998, the production of flowers and fruits in sierra palms was reduced for at least the first 10 months (Zimmerman & Covich, 2007). The lowlands of Tafua's Samoan rainforest suffered 53% tree mortality as a combined effect of two cyclones, whereas the remaining standing trees were severely damaged and the canopy cover was substantially reduced from 100% to 27% cover (Elmqvist, 1994). Furthermore, a survey on eleven species of howler monkeys' feeding trees revealed 35% tree mortality in southern Belize after Hurricane Iris (Pavelka & Behie, 2005). Although in some cases there can be extensive damage to forest vegetation without immediate high tree mortality (Brokaw & Walker, 1991), tree mortaility should be monitored in the following years to reveal the effect at the community level (Everham & Brokaw, 1996). There is clearly variation in the extent of damage that hurricanes can cause on forests and ecosystems and it is not necessarily related to the intensity of the storm (Lugo, 2000).

Obviously, the changes to the forest structure have implications for the animals living in it, which have been documented for invertebrates and different classes of vertebrates. The majority of the studies on the effect of hurricanes on animal populations have been carried out in the Luquillo Experimental forest, Puerto Rico, after Hurricane Hugo devastated the island. The density and distribution of three species of common invertebrates substantially declined in the Luquillo Experimental forest after the passage of Hurricane Hugo, whereas three other species of invertebrates disappeared (Willig & Camilo, 1991). In spite of this report, insects probably both survive hurricanes better than other animals and are able to recover quickly in disturbed forests. Waide (1991) reported outbreaks of black flies, moths and some aquatic insects shortly after Hurricane Hugo. Birds typically respond to hurricanes by moving from heavily damaged sites into protected areas (Wiley & Wunderle, 1993), particularly since strong winds often result in the creation of a patchwork of sites showing different levels of disturbance even within the same forest (Wunderle, Lodge & Waide, 1992; Wunderle 1996). In Maricao State forest, Puerto Rico, the relative abundance for most resident bird species had not recovered 22 months after Hurricane Georges (Tossas, 2006). Moreover, a typhoon affected the distribution and species composition between the open- and continuous-canopy settings, and forest edges and interiors, on the Hengchun Peninsula, Taiwan (Lee, Kuo, Lin, Chu, Wu, Wang & Chao, 2008).

The impact of intense tropical storms has also been studied on populations of amphibians and reptiles (frogs, Woolbright, 1991; lizards, McCoid, 1996; Reagan, 1991; geckos, Ineich, 2010) and bats (Gannon & Willig, 1994; Fleming & Murray, 2009), with mixed outcomes. A survey of 10 species of reptiles following two severe typhoons in the Mariana Islands revealed initial declines in population numbers; however the animals coped better in areas of the surveyed island that represented intact forest prior to the typhoons. Three species of fruit eating bats (*Stenoderma rufum, Artibeus jamaicensis, Bracyphylla cavernarum*) suffered sharp drops in number immediately following Hurricane Hugo and had to increase their foraging range several fold to secure sufficient food supplies (Gannon & Willig, 1994). Conversely, a study focussing on the genetic diversity and population numbers of fruit eating bats (*Erophylla sezekorni, Macrotus waterhousii, A. jamaicensis*) after Hurricanes Ivan, Jeanne and Frances in 2004 showed little

evidence of disturbance, and geckos appear to benefit from severe habitat disturbance as it creates additional breeding sites (Ineich, 2010).

6.1.1 Hurricane impacts on primates

Less research attention has been paid to how primates have fared in the aftermath of hurricane and cyclone activity, and what little is known suggests a less mixed picture. Black and white ruffed lemurs (*Varecia variegata editorum*) responded to an 85% loss of canopy cover, and corresponding decrease in their usual fruit foods following a devastating cyclone, by switching to fruits from other forms of vegetation like shrubs and bushes (Ratsimbazafy, 2006). The long-term impact of cyclone damage appeared to be ultimately responsible for complete group fission in several communities of toque macaques (*Macaca sinica)* (Dittus, 1988).

The most complete study is on black howler monkeys (*Aloutta pigra*) that were adversely affected by Hurricane Iris (Pavelka, et al., 2003; Pavelka & Behie, 2005; Pavelka, McGoogan & Steffens, 2007). Iris was a category 4 hurricane that struck the southern Belize coast on 8 October 2001 with wind speeds exceeding 225 km/hr (Avila, 2001). Hurricane Iris had a devastating impact on the population density of howler monkeys in Belize, which declined by 40% four months after the hurricane (Pavelka, et al., 2003). This was attributable to the 52% decline in the trees providing the howler monkeys' food supply (Pavelka & Behie, 2005). In the dry season following the hurricane, the howler monkeys reliance on leaves shifted from 43% of their diet to 99.8% because of the lack of fruits and flowers (Behie & Pavelka, 2005). Furthermore, the howler monkeys' activity budgets changed as they became more inactive in the dry season following the hurricane (Behie & Pavelka, 2005). This shift in diet and activity budget is not too surprising given that the howler monkey diet comprises a high proportion of leaves and in some populations over 90% of the diet is comprised of leaves (Di Fiore & Campbell, 2007).

During my first field season category 4 Hurricane Emily made a direct hit on the field site at Punta Laguna on 17 July 2005. This was followed by category 5 Hurricane Wilma, which also made a direct hit to the field site on 21 October 2005. These two events hampered my data collection in several respects, although the two hurricanes provided the opportunity to investigate the spider monkeys' behavioural

response to such disturbances, as I could compare data collected on the same individuals in the weeks and months prior to the hurricanes with matched time periods following the hurricanes.

Spider monkeys live in social organisations characterised by a high degree of fission-fusion dynamics (FF dynamics), which is an adaptation for adjusting (sub)group size having evolved as a means to exploit food sources more efficiently and reduce competition over patchy food resources (Kummer, 1971; Aureli et al., 2008; Chapter 1). Given that the two hurricanes were likely to reduce the fruit availability in the monkeys' home range, as previously shown in other Caribbean areas (Pavelka & Behie, 2005, Zimmerman & Covich, 2007), food competition among the spider monkeys was likely to increase. Therefore, the advent of the two hurricanes provided a natural experiment in which to test the effectiveness of FF dynamics.

6.1.2 Aims of the study

The first aim of the present study was to investigate the extent of damage caused by the hurricanes. The second aim was to examine whether spider monkeys' feeding ecology changed in response to a disturbed habitat and whether these changes had an impact on their activity budgets. The third aim was to examine how the monkeys coped with a dramatic decrease in food resources. I predicted that if FF dynamics serve to facilitate the exploitation of limited resources, then the monkeys should be in smaller subgroups in the periods following the hurricanes relative to pre-hurricane periods. Furthermore, I predicted that there would be less fusion events in the post-hurricane period than in pre-hurricane periods. If these two proposed predictions are supported, it would demonstrate effective conflict management during a period when conflicts among individuals would be expected to be higher compared to other periods.

6.2. Methods

6.2.1 Subjects

The subjects included all individuals more than three years of age from the Eastern and Western communities (see Chapter 2, section 2.3)

6.2.2 Procedure

One week following Hurricane Emily I conducted a survey of the damage on 198 representative feeding trees that were normally sampled for phenological status once per month. The number of surveyed trees was equally distributed in the home ranges of the two communities. The state of each tree was defined by one out of four qualitative categories: 1) uprooted tree: the tree was eradicated; 2) loss of primary branches; 3) defoliated: loss of most of the foliage, and 4) no damage.

The analysis of the disturbance brought about by the hurricanes on the activity budget and diet of spider monkeys was performed in two ways. The first analysis (labelled as "immediate effect") focussed on the immediate consequences of Hurricane Emily on spider monkeys' behaviour by comparing the activity budget and diet in the eight weeks preceding the hurricane with eight weeks following the hurricane starting on the 26th of July (given the inaccessibility and potential danger of walking through the forest in the immediate aftermath of the hurricane). The loss of primary branches from many trees created the opportunity for the spider monkeys to forage on the ground for fruit as long as the fruit remained ripe and the patches were not depleted. To control for an effect of that phenomenon on the activities and diet of spider monkeys I repeated the analysis during the same period of time, but excluding the first week of post-hurricane observation when ground feeding was exceptionally common (labelled as "without ground feeding"). The second analysis focussed on a broader period controlling for the seasonal effect of food availability by comparing the pre-hurricane 2005 dry season (January to April) with the post-hurricane 2006 dry season (labelled as "dry season comparison").

The following activities collected with instantaneous scan sampling during focal samples were used for all pre-/post-hurricane comparisons: social (comprised of grooming), resting, feeding and moving (see Chapter 2, section 2.5).The remaining activities (drinking, scanning, self touching, copulation, dangling, attack

and play and other social behaviour were all collapsed in the category "other"). Feeding was subdivided into the type of item consumed (fruits, leaves, flowers, or insects). Fission and fusion events (see Chapter 2 for definitions) were collected on an all occurrences basis (Martin & Bateson, 1993).

6.2.3 Statistical Analysis

Proportions of activity scans were used for the comparison of the time budgets before and after the hurricanes. I also compared the proportions of type of food (fruits, leaves, flowers, larvae and other) consumed out of the total scans spent feeding. Paired sample t tests or Wilcoxon signed rank tests were used in accordance with the distribution of the data. For Wilcoxon sign rank tests, when the N was less than 15 the T and corresponding p values were presented, whereas when the N exceeded 15 the z and asymptotic p values were presented (Siegel & Castellan, 1988).

To investigate whether the ecological damage brought about by the hurricane(s) influenced the subgroup size, two measures were used: 1) the number of individuals in the first subgroup encountered on each observation day, and 2) the number of individuals in the first subgroup encountered between 11:30-12:30 hrs. To compare subgroup patterning before and after the hurricane(s) I used three measures of FF dynamics. The first measure, the mean daily subgroup size, was given by dividing the sum of subgroup sizes by the number of subgroups formed during each observation day. The second measure, hourly fusion rate, was given by the number of fusion events per hour for each observation day. Finally, for the dry season comparison only I calculated the proportion of days for which no fusion events were observed and presented the descriptive results. For the other comparisons, I used independent t tests or Mann-Whitney U tests according to the distribution of the data. For all statistical tests, p value of 0,05was adopted, unless I made multiple comparisons among related dependent measures, then the Bonferonni correction was applied.

6.3 Results

Seventy two percent of the 198 sampled trees were physically damaged after Hurricane Emily (Figure 6.1), 32% had serious damage, 40% were completely defoliated and 28% had little or no damage.

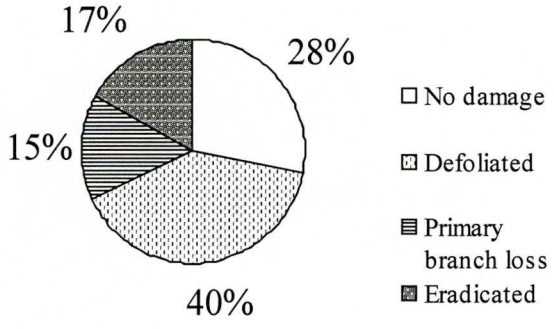

Figure 6.1 The percentage and type of damage to trees by hurricane Emily (N=198).

6.3.1 Activity budgets and diet

6.3.1.1 Immediate effect of Hurricane Emily

When I analysed the immediate effect of Hurricane Emily on the activity budget, I found that spider monkeys moved less after than before the hurricane (ties=0, n=21, T=18, p=.001). There was no significant difference for the other activities [social: ties=8, n=13, T=66, p=.15; feeding: $t(20)$=-1.38, p=.183; resting: $t(20)$=-.985, p=.34; Figure 6.2].

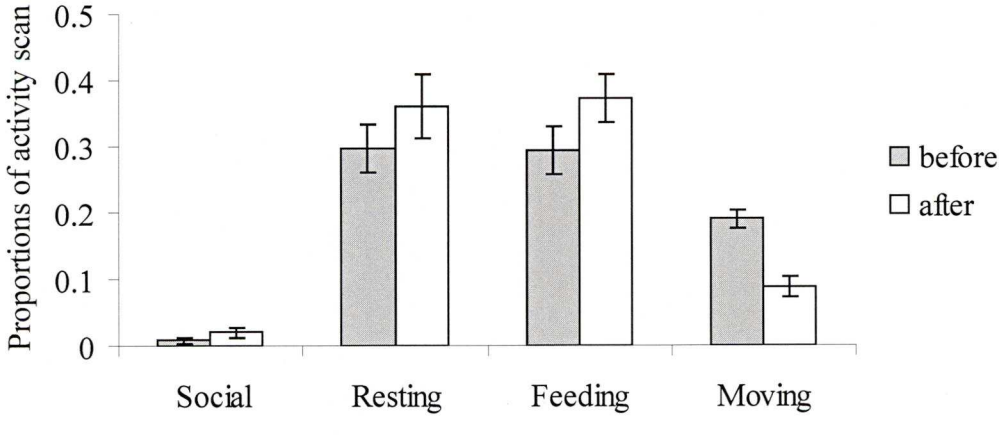

Figure 6.2 Mean (±SE) proportions of activity scans immediately before and after the hurricanes (N=21) * = significant difference between pre and post hurricane periods.

Individuals relied significantly more on leaves immediately after the hurricane compared to before [$t(16)=4.144$, $p=.001$)], and consumption of other food items was higher before the hurricane compared to after (ties=14, $n=4$, $T=2$, $p=.002$). I found no difference for the consumption of fruits [$t(16)=.044$, $p=.966$] and flowers (ties=15, $n=3$, $T=1.00$, $p=.285$).

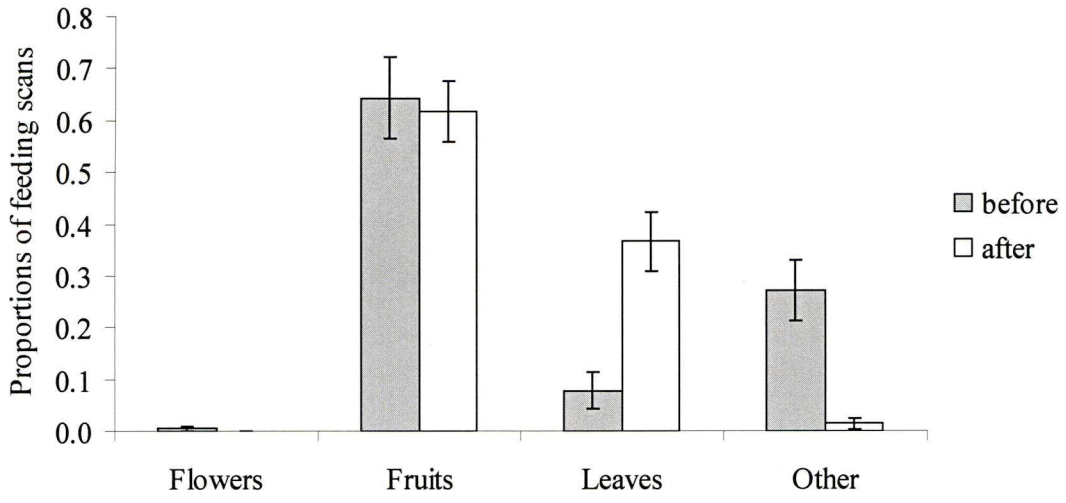

Figure 6.3 Mean (±SE) proportion of feeding scans spent eating different food items immediately before and after the hurricane (N=18). * = significant difference between pre and post hurricane periods.

When I repeated the analysis excluding the days of "ground feeding", the overall pattern of results did not change. I found a significant difference for moving [$t(19)=7.620$, $p< .001$] as individual moved less after than before the hurricane. No differences were found for the remaining activities [feeding: $t(19)= 1.72$, $p=.102$; resting: $t(19)=1.17$, $p=.26$; social: ties=8, $n=12$, $T=63$, $p=.06$, Figure 6.4)]. In addition, the increase in the consumption of leaves was still significantly higher after than before the hurricane [$t(16)=4.144$; $p=.001$], whereas other food items were consumed significantly more before the hurricane (ties= 4, $n=13$, $T=2$, $p=.002$). No difference were found for fruits and flowers [fruits: $t(16)=-.044$; $p=.97$; flowers: ties= 14, $n=3$, $T=1$, $p=.29$; other: Figure 6.5].

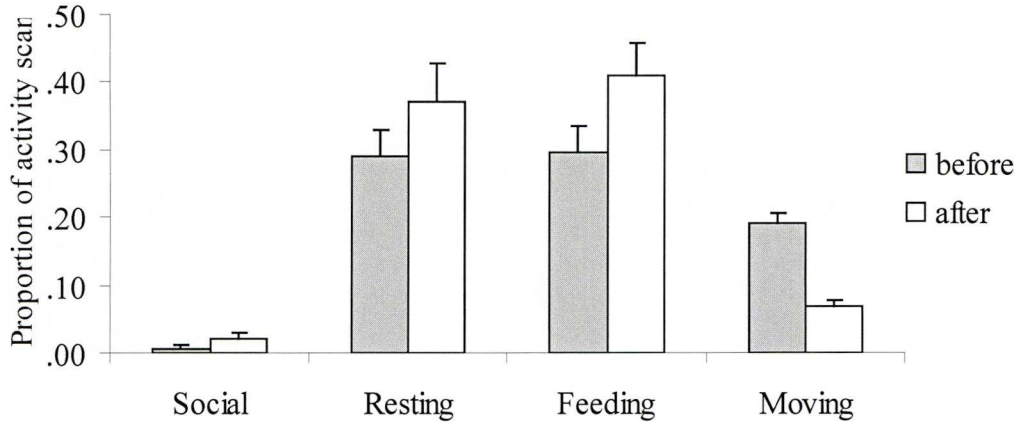

Figure 6.4 Mean (±SE) proportion of activity scans immediately before and after hurricane Emily without ground feeding (N=20). * = significant difference between pre and post hurricane periods

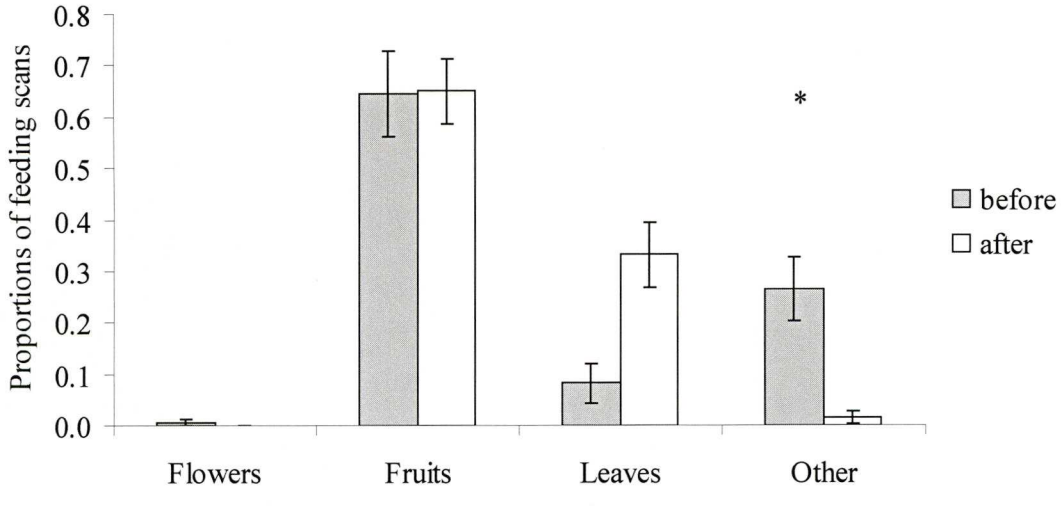

Figure 6.5 Mean (±SE) proportion of feeding scans spent eating different food items immediately before and after hurricane Emily without ground feeding (N=17). * = significant difference between pre and post hurricane periods.

6.3.1.2 Dry season comparisons

The comparisons between the dry seasons revealed that the proportion of moving was lower after the hurricanes [$t(24)=1.70$, $p=.004$] while the proportion of resting was higher after the hurricanes [$t(24)=3.52$, $p=.002$; Figure 6.6] The remaining behaviours were not significantly different between the two dry seasons [social: $t(24)=1.70$, $p=.102$; feeding: $t(24)=1.02$, $p=.32$; Figure 6.6].

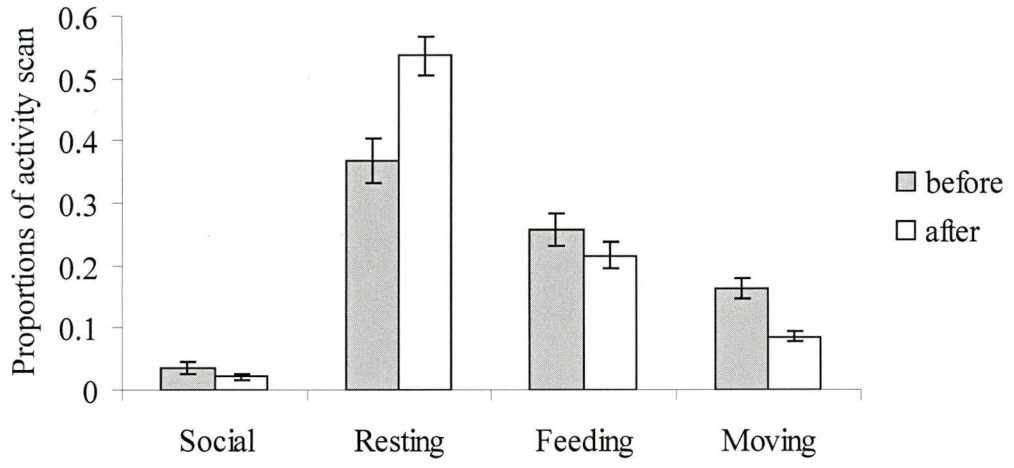

Figure 6.6 Mean (±SE) proportions of activity scans during the dry season before and after the hurricanes (N=25). * = significant difference between pre and post hurricane periods

In the dry season following the two hurricanes the proportion of scans spent eating fruits was significantly lower [$t(22)=6.85$, $p<.001$], whereas that for leaves was significantly higher [$t(22)=-7.19$, $p<.001$] than in the dry season before the hurricanes (Figure 6.7). I found a tendency for flowers to be eaten less after the hurricanes (ties=12, $n=11$, $T=12.00$, $p=.062$). No difference was found for other food items (ties=11, $n=12$, $T=38.00$, $p=.937$).

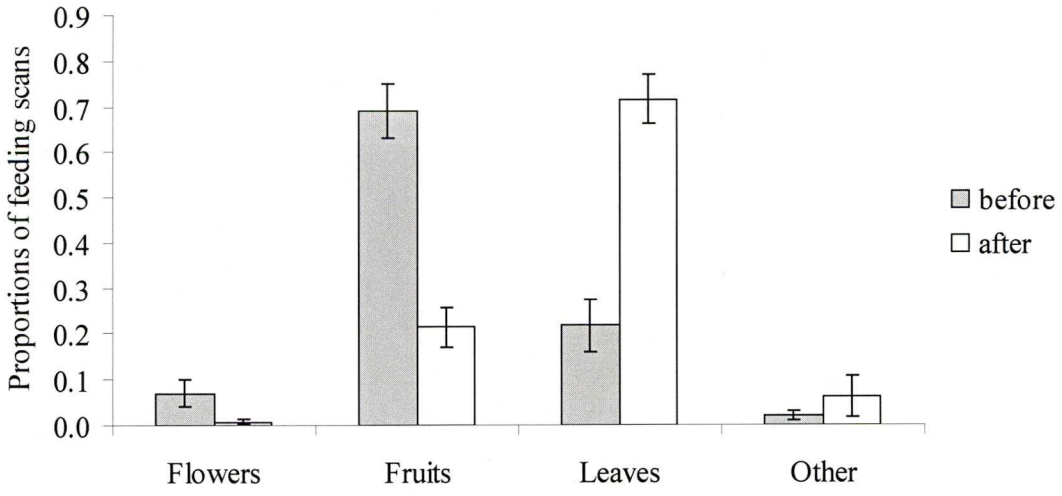

Figure 6.7 Mean (±SE) proportion of feeding scans spent eating different food items during the dry season before and after the hurricanes (N=23). * = significant difference between pre and post hurricane periods

6.3.2 Subgroup size

Subgroup size of the first subgroup encountered on each observation day was significantly smaller immediately after than immediately before Hurricane Emily [N_1=29, N_2=32, U=212.0, Z=-3.81, p <.001; Figure 6.8]. The same test was performed excluding from the analysis the first week following the hurricane during which spider monkeys were feeding on the fruit that had fallen on the ground and therefore may not have adjusted their subgroup size as fruit was still abundant. I found that subgroup size of the first encountered subgroup was still significantly smaller immediately after than before the hurricane [N_1=18, N_2=20, U=187.0, Z=-3.43, p=.001, Figure 6.8]. Similarly, the subgroup size of the first encountered subgroup was significantly smaller in the dry season after the hurricanes compared to the dry season before the hurricanes [N_1=60, N_2=41, U=910.5, Z=-2.51, p=.012, Figure 6.8].

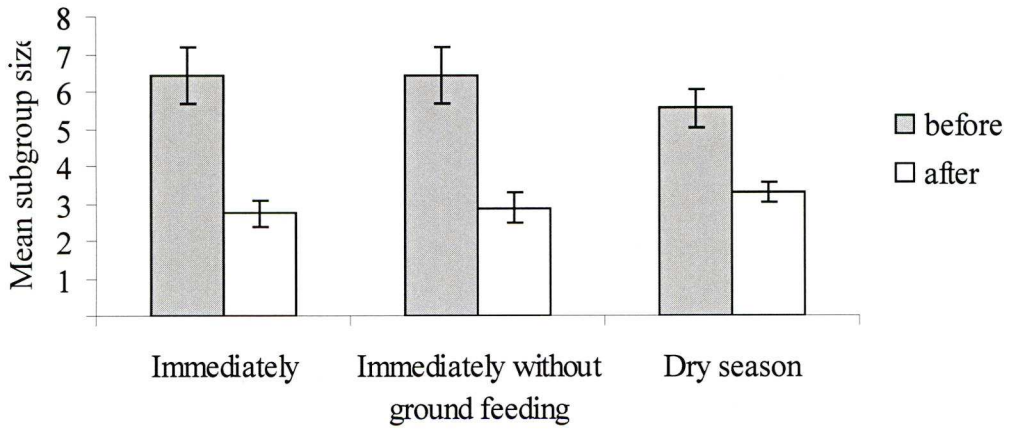

Figure 6.8 Mean (±SE) subgroup size of first subgroup encountered on each observation day before and after hurricane. Immediately: N_1=29, N_2=32; Immediately without ground feeding: N_1=18, N_2=20; Dry season: N_1=60, N_2=41. * = significant difference between mean subgroup size before and after the hurricane(s).

When I compared the size of the first subgroup encountered between 11:30 and 12:30 hrs each observation day, it was significantly smaller immediately after than immediately before the hurricane [t(21)=2.22, p=.038, Figure 6.9]. This result held when I excluded the first week following the hurricane [t(12)=2.34, p=.038, Figure 6.9]. A similar difference was found between the dry season before the

hurricanes and the dry season after the hurricanes [N_1=21, N_2=18, U=107.50, Z=-2.45, p=.014, Figure 6.9].

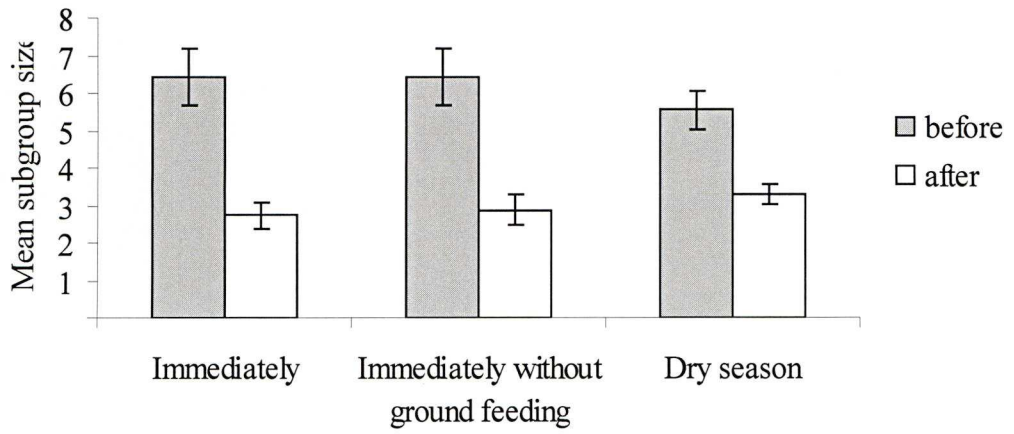

Figure 6.9 Mean (±SE) subgroup size of first subgroup encountered between 11:30 and 12:30 hrs each observation day before and after hurricane. Immediately: N_1=12, N_2=11; Immediately without ground feeding: N_1=7, N_2=7; Dry season: N_1=21, N_2=18. * = significant difference between mean subgroup size before and after the hurricane(s).

Furthermore, the mean daily subgroup size was smaller after than before the hurricane in each of the three analyses using a different temporal scale [immediate period: $t(59)$=4.64, p <.001; immediate period without ground feeding: $t(36)$=6.09, p<.001; dry season: $t(99)$=3.42, p=0.001; Figure 6.10].

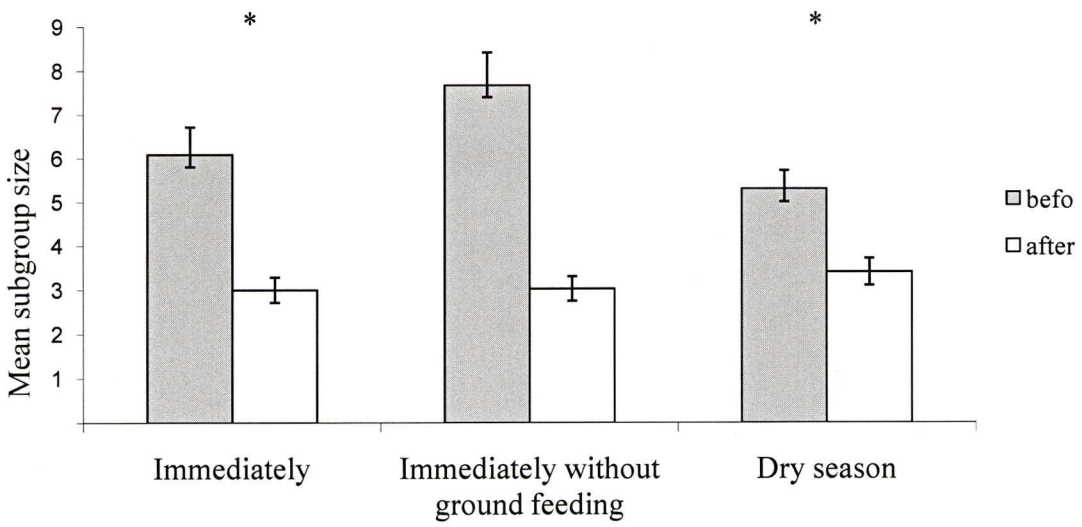

Figure 6.10 Mean (±SE) daily subgroup size before and after the hurricane. Immediately: N_1=29, N_2=32; Immediately without ground feeding: N_1=18, N_2=20; Dry season: N_1=60, N_2=41.* = significant difference between before and after the hurricane.

Hourly fusion rates were not significantly different between periods immediately after and before the hurricane ($t(55)=1.07$, $p=.085$; without days of ground feeding $t(50)=1.17$, $p=.056$, Figure 6.11). However, fusion rates were lower during the dry season after the hurricane compared to the dry season before the hurricanes [$N_1=61$, $N_2=41$, $U=960.50$, $Z=-2.042$, $p=.041$].

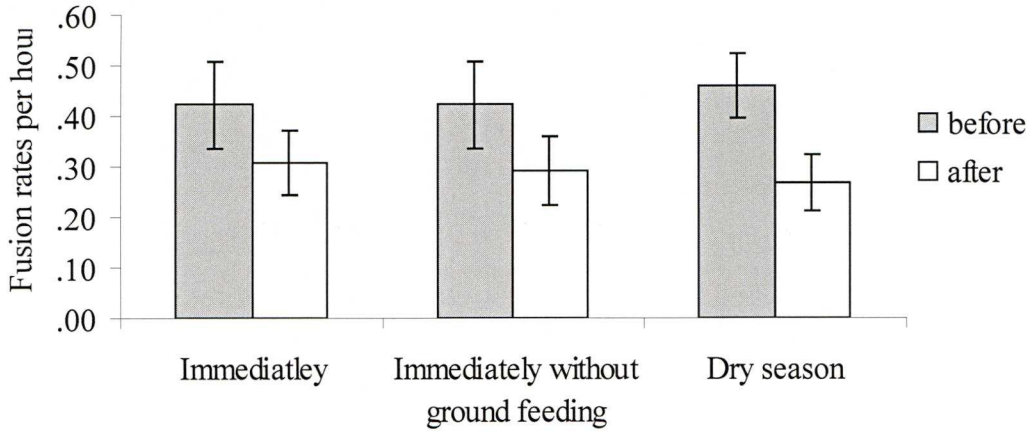

Figure 6.11 Hourly fusion rates during the dry season before and after the hurricane, just before and after the hurricane, just before and after the hurricane without days of ground feeding. Immediately: $N_1=27$, $N_2=30$; Immediately without ground feeding: $N_1=27$, $N_2=25$; Dry season: $N_1=61$, $N_2=41$. * = significant difference between pre and post hurricane periods.

Aggression seemed to be managed well by the changes in subgrouping dynamics. I witnessed 26 aggressive events in the dry season before the hurricanes, compared to only 3 aggressive events in the dry season after the hurricane. The rate of aggressive events per hour in the dry season before the hurricane was of .107, whereas a rate of only .021 was found during the dry season following the hurricanes.

6.4 Discussion

The first aim of the study was addressed as I was able to document the extent of the damage to the monkeys' habitat. I found that over 70% of the trees had experienced such extensive damage that they would be unable to produce fruit in the immediate aftermath of the hurricanes. The second aim, to examine whether spider monkeys'

feeding ecology changed in response the hurricanes and whether the changes had an impact on their activity budgets, was also addressed. In the immediate aftermath of the hurricane the spider monkeys were observed eating leaves during more scan samples than prior to the hurricane and they also moved significantly less than prior to the hurricane. These changes did not alter when I removed the data from the first few days following the study when the spider monkeys used the ground to forage on fallen fruits. In addition, the monkeys' reliance on food shifted dramatically when I compared the dry season before and after the hurricanes. The proportion of scans in which they fed on fruits decreased from 70% of scans in the dry season before the hurricanes to 20% in the dry season after the hurricanes. In the latter season, the spider monkeys relied heavily on emerging leaves, which accounted for 70% of all feeding scans. There was also a change in the distribution of their activity budgets as the monkeys were observed resting more and moving less in the dry season after the hurricanes. The third aim of my study was to examine whether there was evidence of any conflict management strategies adopted by the monkeys in the aftermath of the hurricanes. My predictions were supported as the monkeys were in smaller subgroups following the hurricanes relative to pre-hurricane periods and the monkeys fusioned less often in the dry season following the hurricanes compared to the dry season before the hurricanes.

6.4.1 Habitat damage

In the natural protected area of "Otoch Ma'ax Yetel Kooh" the vast majority of trees suffered damage due to the strong winds of Hurricane Emily. The most common damage was defoliation, whereas 32% of trees had more severe damage. The extent and type of damage mirrors those reported for other forests struck by hurricanes and other cyclonic storms (Dittus, 1985; Brokaw & Walker, 1991; Pavelka, et al., 2003; Bonilla-Moheno, under review). However, the damage evaluation conducted on a forest in the state of Quintana Roo, Yucatan Peninsula, after Hurricane Gilberto showed that all trees were damaged and most had only their largest branches remaining (Whigham, Olmsted, Cabrera-Cano & Harmon, 1991). Also the damage brought about by Hurricane Iris on the Belize coast provided a rather dramatic scenario where all trees were 100% defoliated (Pavelka & Behie, 2005). In contrast, after Hurricane Emily 28% trees did not sustain major damage. However, the

temporal closeness of a further hurricane, only three months apart from Emily, provoked additive defoliation impact on 25% of the remaining undamaged trees, meaning that only 21% of the trees remained undamaged in the post-hurricane dry season (Bonilla-Moheno, under review).

6.4.2 Activity budgets

The analysis of the activity budget of spider monkeys after Hurricane Emily showed that individuals significantly reduced the time spent moving. The same result was obtained when excluding the "ground feeding days" demonstrating that the effect on time spent moving was not driven by those days in which fruit harvesting on the ground was common. A similar change in activity pattern was found for red colobus monkeys (*Colobus badius rufomitratus*) in a fragmented habitat, which arose from increases in agricultural activity and an altered course of a river, and was related to a dietary change towards foods with higher content of fiber and tannins (Decker, 1994). Furthermore, a study on the patterns of activity in response to Hurricane Iris revealed that howler monkeys spent more time inactive after the hurricane compared to pre-hurricane periods. Their inactivity was ascribed to the vast amount and distribution of new leaves that represented their main feeding resource in the disturbed forest and allowed individuals to feed without needing to travel (Behie & Pavelka, 2005). In my study the reduced time spent moving, particularly in the dry season after the hurricanes, is also likely due to the change in forest structure which affected food availability. Similarly to what affected the activity budget in howler monkeys, the drastic reduction of fruits and flowers is likely responsible for the high folivory of spider monkeys in post-hurricane periods. Indeed spider monkeys in this study consumed a significantly higher amount of leaves after the hurricane. Furthermore, the increase of leaf buds produced by trees after the hurricane may have contributed to the reduction in moving activity. Typically, new leaves and sprouting of new branches appear on surviving trees (Brokaw & Walker, 1991; Bonilla-Moheno, under review). Spider monkeys rarely eat mature leaves and prefer immature leaves (di Fiore & Campbell, 2007). Thus, the concentrated distribution of buds and young leaves allowed individuals to gain nutritional requirements without needing to travel long distances. This is especially relevant when high quality food is

scarce. Spider monkeys are known to travel long distances in Yasuni National Park, which is characterised by an extremely diverse environment, where the cost of travel is compensated by a variety of high quality fruits (Suarez, 2006). Conversely, the food easily available during the post-hurricane dry season at my field site was of too low quality to make long distance travel worthwhile.

The comparison of activity budgets between the dry seasons before and after the hurricanes revealed that spider monkeys not only spent less time moving, but also spent more time resting. This is also probably related to the scarcity of fruit and the high amount of leaves available after the hurricanes, as discussed above, which exacerbated the paucity of food resources typical of the dry season. Spider monkeys during the dry season range over a smaller area, repeatedly visiting a few intensively used fruiting trees (Nunes, 1998). Thus, the difference of activity budgets between the two dry seasons is a further indicator that the impact of hurricanes on the forest structure created a much more severe fruit shortage, than the typical reduction of fruiting species during the dry season.

The increase of resting activity during the dry season after the hurricanes is probably a consequence of reduced moving, thus individuals have more time to spend resting. However, among other factors that could affect resting time are longer digestive times associated with a higher leaf intake. Spider monkeys' digestive system is indeed designed essentially for easily digestible foods like fruits (Gonzalez-Zamora, et al., 2009) and *A. geoffroyi* are known to have a relatively short gut passage time that would not favour optimal digestion of leaf matter (Milton, 1981). Leaves are a much poorer quality food when animals do not have the physiological adaptations to ferment leaves, which are necessary to extract maximum energy gain (Milton, 1981). Therefore, spider monkeys may have to rest because of a lack of sufficient nutrient intake. Indeed, Milton (1981) suggests that the spider monkey gut physiology would make reliance on a predominantly leaf based diet almost impossible. This latter explanation is supported by the fact that no difference was found in resting time in the comparison of the periods immediately before and after Hurricane Emily as some residual fruits were available during that period. Furthermore, shade loss due to reduced canopy cover and consequent increased temperature might increase the proportion of time spent resting (Fernandez &

Fletcher, 1991) and was a factor thought to influence the increased resting in howler monkeys following Hurricane Iris (Behie & Pavelka, 2005).

In all three comparisons at different temporal scale, leaves were consumed significantly more often after the hurricane(s). Furthermore, in the dry season comparison fruits were consumed significantly less after the hurricane. Spider monkeys are highly frugivorous with fruits accounting for more than 70% of their diet (Russo, Campbell, Dew, Stevenson & Suarez, 2005; di Fiore & Campbell, 2007; di Fiore, et al., 2008), although Gonzalez-Zamora (2009) reported that *A. geoffroyi* is slightly less frugivorous compared to other South American Atelines. Nevertheless, the drastic change in food items consumed after the hurricane was a clear way to cope with an altered forest structure, where fruits were reduced and leaves were widely distributed. Similar results have been found for other primates in disturbed habitats and represent some degree of dietary flexibility. Although, predominantly folivorous, howler monkeys typically devoted 38% of their feeding time to fruits, whereas they became completely folivorous in a hurricane degraded habitat (Behie & Pavelka, 2005). Long-tailed macaques (*Macaca fascicularis*) and red colobus monkeys were forced to fall back on less preferred food items in highly disturbed habitats (Bernstain, 1986; Decker, 1994). Dietary flexibility has been also demonstrated by individuals in a highly frugivorous primate community in the Lopé Reserve, central Gabon, during long periods of crop failure and fruit scarcity. Eight species of primates (lowland gorillas, *Gorilla g. gorilla*; chimpanzees, *Pan troglodytes*; mandrills, *Mandrillus sphinx*; black colobus monkeys, *Colobus satanas*; Grey cheeked mangabey, *Cercocebus albigena*; putty-nosed guenons, *Cercopithecus nictitans*; crowned guenons, *C. pogonias*; mustached guenons, C. *cephus*) changed their diet by relying more on leaves, flowers and insects in response to fruit scarcity (Tutin, Ham, White & Harrison, 1997). Some species however show somewhat less flexibility under changing habitat conditions. For example, vervet monkeys (*Chlorocebus aethiops*) did not incorporate new foods into their diet in a changing habitat, but largely maintained a similar degree of dietary diversity over a nine year period, slightly adjusting their diet to the available food (Lee & Hauser, 1998). Similarly, when a cyclone reduced the availability of fruit in their habitat black and white ruffed lemurs (*Varecia variegata editorum*) remained predominantly

frugivorous and diversified their diets only in terms of the variety of fruit species consumed (Ratsimbazafy, 2006).

Spider monkeys are known for having a somewhat flexible diet as it is related to the temporal distribution of the feeding resources such that plant species are generally selected on the basis of their availability (Nunes, 1998; Russo et al., 2005). Spider monkeys do show preference for a small number of fruiting species, but use other species in an opportunistic way (Symington, 1988; Nunes, 1998; Wallace, 2005). The flexibility of spider monkeys' diet has been previously demonstrated by the proportionally greater amounts of leaves consumed in small unprotected forest fragments (55%) compared to large protected forests (14%) (Gonzalez-Zamora et al. 2009). In addition, in two populations of *A. belzebuth chamek* leaf consumption was negatively correlated with availability of ripe fruits (Di Fiore, et al., 2008). Thus, lower-quality plant vegetative parts were consumed when preferred higher-quality resources were scarce. These results indicate that spider monkeys are opportunistic feeders able to adapt to the best option offered by their hosting habitat. Even in highly degraded habitats spider monkeys are able to cope with fruit shortage by switching to foods of lower energetic content such as leaves. However, it is not yet clear to what extent spider monkeys are capable of relying on almost complete folivory. Wallace (2005) reported that high folivory had negative consequences on spider monkeys' body conditions and *Ateles'* digestive system might not be able to tolerate long-term folivory (Milton, 1981).

During the periods immediately before Hurricane Emily, individuals consumed other type of food items significantly more than after. The category "other" includes larvae which account for the significant difference obtained. In my study the consumption of larvae was only found immediately before Hurricane Emily and in the dry season after both hurricanes. Overall, insects constitute a very small proportion of the annual diet of *Ateles*. The consumption of caterpillars has been reported in several study populations (Link, 2004) and seems to be associated with a few species that massively bloom in specific host trees. The consumption of caterpillars has been reported to occur only during relatively short time frames, such as one or two weeks a year (Di Fiore, Link & Dew, 2008), and appears to be the same for my study population (Aureli, Ramos-Fernandez, Schaffner & Vick,

unpublished data). Therefore, it is possible that Hurricane Emily came across one of these periods of caterpillar blooming. The impact of the hurricane swept away all the leaves and the caterpillars with them. Consequently, immediately after the hurricane no caterpillars were available. However, insect populations recover relatively quickly after hurricanes (Waide, 1991). The persistence of larvae and pupae in sheltered retreats together with high temperatures, nutrient rich litter and new leaves flushing on defoliated trees provide favourable conditions for insects to reproduce. Thus, it is possible that during the dry season following the hurricanes spider monkeys could feed on caterpillars which probably represented one of the most high quality foods available given the scarcity of fruits due to long recovery times.

6.4.3 Subgroup dynamics

The effect of hurricanes on subgroup dynamics was investigated through measures of subgroups size and fusion events. My hypothesis, that the spider monkeys would have smaller subgroups following the hurricane was supported for all three measures of subgroup size (first subgroup encountered in the day, first subgroup encountered between 11:30-12:30 and mean daily subgroups size). I found significantly smaller subgroups in post-hurricane observations compared to pre-hurricane observations. Thus, all three measures of subgroup size were consistent in indicating the impact of hurricanes on subgroup size. Furthermore, the prediction that subgroups would be less likely to fusion together in the post-hurricane period was also supported. Fusion events were less frequent in the dry season following the hurricanes compared to the dry season before the hurricanes.

The reduction in subgroup size is likely a response to decreased food availability. As a general rule, in larger groups intra-group feeding competition and travel cost increase under conditions of low food availability (Symington, 1988). In spider monkeys, dispersion and association patterns are related to seasonal variation in food supply (Wallace, 2008). Fission-fusion dynamics allow spider monkeys to adjust subgroup size to local food availability, so that when they are in larger subgroups competition does not increase and they do not experience greater travel costs compared to when they are in smaller subgroups (Asensio, et al., 2008; Asensio, et al., 2009). Thus, the smaller subgroup size in post-hurricane periods could be seen as an extension of such a strategy to cope with the dramatic food

scarcity and potential increased risk of intra-community competition over limited resources. The decreased rate of fusion events during the dry season after the hurricanes likely reflects a general tendency for individuals to spend more time separated from other community members to avoid the higher costs of being in a larger subgroup in such a disturbed habitat. The reason of the non-significant decrease in hourly fusion rates in the immediate aftermath of Hurricane Emily could lie in the possibility that individuals were still adapting to the ecological changes and exploring the new environment in search of fruit leftovers.

The few studies that documented the effect of degraded habitats on the foraging patterns and group cohesiveness of primates revealed similar patterns. Solitary individuals were more common in black howler monkeys and ruffed lemurs after a hurricane and a cyclone, respectively (Pavelka et al., 2003; Ratsimbazafy, 2006; Pavelka, et al., 2007), although the initial decline in the howler monkey population was attributed to mortality in the aftermath of Hurricane Iris. Howler monkeys' mean social group decreased from 6.6 to 4 individuals three and a half years after a Hurricane Iris (Pavelka, et al., 2007). Furthermore, low-ranking female toque macaques (*M. sinica)* fissioned from their group to form a separate and permanent independent group in response to increased intra-group competition arising from habitat fragmentation due to a cyclone in 1978 that destroyed 40% of the canopy (Dittus, 1988; 2004). In addition, long-tailed macaques split into subgroups to better exploit widely dispersed food sources in a degraded habitat (Bernstain, 1986). Thus, drastic changes in the environment can undermine social cohesiveness. In exceptionally degraded habitats different species, depending on their degree of FF dynamics (Aureli et al., 2008), can opportunistically be less cohesive and exploit solitarily or in small subgroups scarce and scattered feeding resources, or instead fission permanently and form a new group. Animals living in groups characterised by high degree FF dynamics might be facilitated in the response to drastic changes in food availability and distribution (Tutin, et al., 1997). Thus, in periods of prolonged scarcity spider monkeys' subgrouping patterns are adjusted to food availability, which represents an effective strategy to cope with potentially increased intra-group competition. In other words, spider monkeys' ability to adapt to varying habitat conditions is driven by a well-established mechanism through which conflicts of interest are avoided without renouncing to most of the benefits of

sociality. Indeed, in my study aggressive conflicts in the dry season after the two hurricanes the aggression rate was five times lower than the corresponding rate in the previous dry season, which supports the effectiveness of small subgroups during a period of low resource availability. Furthermore, the small subgroup size found immediately after Hurricane Emily suggests that the high FF dynamics of spider monkeys' provided them with a natural tool to cope in the emergency caused by Hurricane Emily. By contrast howler monkeys that live in more cohesive groups experienced a period of social disorganization, in terms of transient individuals, large number of solitary monkeys and small fragmentary groups, for 12 weeks after Hurricane Iris (Pavelka & Chapman, 2005).

6.4.4 Conclusions

The impact of two hurricanes only three months apart from each other revealed the flexibility of spider monkeys to adapt to a highly degraded habitat characterised by fruit scarcity. Switching to an almost completely folivorous diet, spider monkeys relied on the only food source widely available. The dietary change resulted in different time allocation compared to the pre-hurricane activity budget and in different subgrouping patterns whereby conflict of interest arising from food competition were drastically reduced. Indeed, high FF dynamics are related to ecological factors and dietary niches (Chapman, et al., 1995; Lehman, Korstjens & Dunbar, 2007) and are thought to have evolved in order to reduce competition over patchy resources (Kummer, 1971; Aureli et al., 2008). In the case of spider monkeys that are predominantly frugivorous it means that feeding patches are quickly depleted by foraging animals and thus the number of individuals that can forage on it is constrained by food quantity and distribution. Thus, ranging in smaller subgroups represents a means to avoid competition for food by adapting the subgroup size to high quality food availability (Asensio et al., 2009). The spider monkeys' subgrouping pattern in the aftermath of the hurricanes is accounted for by the proximate mechanism of an evenly distributed, low quality food source (i.e., emerging leaf buds and young leaves), which negated the need for individuals to travel great distances to find patchy unpredictable food sources or possibly made it impossible to do so because of the energy constraints. My finding contributes to our understanding of how such conflict management mechanism can arise, without the

need to invoke a prospective intelligence on the part of the monkeys. The natural experiment offered by the two hurricanes that struck the field site in the middle of my data collection provided a powerful tool to demonstrate how ecological factors have a direct effect on the social organisation of spider monkeys. Subgrouping patterns were quickly adjusted to the disturbed setting and the likely increase of intra-group competition was therefore prevented.

Chapter 7

General Discussion

7.1 Conflict management mechanisms in wild spider monkeys

I set out to investigate conflict management in wild spider monkeys with the aims of identifying the role fission-fusion dynamics (FF dynamics) and relationship quality play in regulating pre- and post-conflict mechanisms. Post-conflict interactions were analysed to examine whether spider monkeys engage in reconciliation, redirection or bystander affiliation. The role of fission was examined to determine whether low cohesiveness provides spider monkeys with an additional strategy to cope with aggressive conflicts. Pre-conflict mechanisms were examined in the context of fusion events, which is a context with a high potential for aggression (Aureli & Schaffner, 2007). The quality of spider monkeys' relationship were obtained by extracting components of relationships representing non-subjective correlations of dyadic interaction. The influence classes of age, kinship, sex, tenure and group membership had on the components of relationship were also determined to enable a greater understanding of spider monkeys dyadic interactions. Furthermore, the effect components of relationships had on pre and post-conflict behaviours provided further insight into the mechanisms regulating social dynamics and conflict management. Finally, a natural experiment presented the opportunity to examine spider monkeys' behavioural flexibility and to investigate how FF dynamics are associated with conflict management.

7.1.1 Pre-conflict mechanisms

The present study confirms that friendly behaviours, including embraces, kisses and pectoral sniffing, serve the function of preventing aggressive escalation in contexts associated with high tension. Fusion events are associated with aggression in chimpanzees and spider monkeys (*Pan troglodytes*, Bauer, 1979; Bygott, 1979; Goodall, 1989; *Ateles* spp, Klein & Klein, 1971; Aureli & Schaffner, 2007). In my study (Chapter 5) the likelihood of aggression increased in the first five minutes following a fusion event. Friendly behaviours were also performed significantly more in the aftermath of a fusion event during the same time window, replicating an earlier study on the same species (Aureli & Schaffner, 2007). In addition, I found

that aggressive and friendly behaviours were performed selectively among members of joining subgroups. This result suggests that a temporal separation might result in uncertainty about the relationship of two individuals, which is in turn responsible for the increased tension. Given that relationships are partly defined by interactions of individuals over time (Hinde, 1976) uncertainty might arise among individuals that were temporarily apart. Post-fusion friendly interactions functioned to reduce a potential increase in post-fusion aggression confirming their function of signalling good intentions and reducing tension. In fact, when post-fusion friendly behaviours were exchanged between members of a joining subgroup, aggression never occurred. The communication of good intentions therefore is an effective strategy to reduce the escalation of aggression. However, prevention of aggressive escalation can be achieved at an even earlier stage of conflict management.

High FF dynamics have evolved in association with patchy distribution of high quality food allowing individuals to adjust subgroup size to the availability of their feeding resource thereby avoiding a high degree of intra-group competition (Kummer, 1971; Chapman, 1990; Symington, 1990; Shimooka, 2003; Lehman et al., 2007; Wallace, 2008). Societies characterised by high FF dynamics represent a pre-conflict management strategy to prevent and reduce conflicts of interest. The flexibility that characterises societies with high FF dynamics has been highlighted by a natural experiment represented by two almost consecutive hurricanes that affected the field site 6.5 months into my data collection. The impact of the two hurricanes on the forest resulted in a drastic, almost total, reduction of fruits in the year following the hurricane, which account for at least 70% of spider monkeys' diet (Russo, et al., 2005; Di Fiore & Campbell, 2007; Di Fiore, et al., 2008). In response to the sudden increase in food competition, spider monkeys dramatically changed their activity budgets by reducing travel and changing from a reliance on fruit to leaves compared to the pre-hurricane period. After the hurricanes the mean subgroup size was significantly smaller compared to pre-hurricane values, suggesting that spider monkeys quickly adjusted to scarce fruit availability to avoid conflicts over food. The decreased rate of fusion events in the dry season after the hurricanes compared to the dry season before reflect the general tendency for individuals to spend more time in small groups separated from other community members and possibly to avoid travel costs associated with larger subgroups.

7.1.2 Post-conflict mechanisms

My study provided evidence that spider monkeys do not engage in reconciliation, redirection or bystander affiliation after aggressive conflict. The only post-conflict behaviour that differed significantly from baseline observation was the shorter latency to fission from former opponent. Individuals were more likely to split from the former opponent within one hour from the aggressive interaction. This is the first time anyone has demonstrated fission as a post-conflict management mechanism. Increased levels of anxiety were exhibited only by victims of aggression during the first five minutes following the conflict suggesting an asymmetry in the perception of the damage caused by the aggressive interaction. Reconciliation is expected to occur when it benefits both opponents (Aureli, et al., 2002). The risk of a renewed aggression may be too high if reconciliation benefits only one of the participants. In this circumstance fission is a viable option to cope with the increased post-conflict uncertainty. The long latency found for fission may be explained by the time individuals might need to await for fissioning with other subgroup members since leaving the subgroup alone might be too costly.

7.1.3 Role of relationship quality in managing conflict

Relatively few studies have been done that examine the quality of relationships in non-human primates using an objective approach. For example, the attempt to qualify relationships has been related to specific aspects of relationships, such as kinship (Maynard-Smith, 1964; Trivers & Hare, 1976; Gouzoules & Gouzoules, 1987; Parker, Waite & Dereck, 1995). More recently, the use of PCA provided a statistical tool to reduce subjectivity and inconsistency by collapsing the correlated behavioural variables into components of relationships. The use of PCA in my study revealed at least two components of relationships identified as Compatibility and Risk. Kinship and sex combination had an effect on compatibility. The effect of kinship was mostly attributed to the association pattern of mother-offspring along with high proximity and grooming rates, as found in other studies for adult and juvenile females likely to be mother-offspring (Fedigan & Baxter, 1984; Ahumada, 1992; Mc Daniel, 1994; Vick, 2008; Slater, et al., 2009). The higher compatibility found for male-male dyads compared to other sex combinations is in line with

current evidence. Indeed male-male relationships are reported as highly affiliative and cooperative (Fedigan & Baxter, 1984; Ahumada, 1992; Wallace, 2001; 2008; Shimooka, 2003; Aureli et al., 2006; Aureli & Schaffner, 2008; Slater et al., 2009). Male-male relationships however, were the most risky compared to other sex combinations. The component of Risk was defined by aggression and embraces. The coexistence of two seemingly conflicting relationships components (Compatibility and Risk) revealed a complicated dimension regarding the nature of male-male relationships, but may reflect variation in the quality of male social relationships that is age-based. Older males may be less tolerant of younger maturing males and my data did demonstrate that those dyads were the most likely to exchange aggression. In addition, previous studies in captivity and the wild suggest older males selective target younger males (captivity, Davis, et al., 2009; wild, Campbell, 2006; Valero, et al., 2006).

Risk and sex combination had an effect on the latencies to fission in the aftermath of a conflict. Male-male dyads and high risk dyads fissioned significantly sooner from former opponents compared to male-female dyads and dyads with less risky relationships. It appears that individuals which are more likely to incur renewed aggression after conflicts are more motivated to leave the subgroup sooner to avoid further aggression and cope with post-conflict anxiety. In addition, more compatible dyads fissioned from each other later in the aftermath of aggression relative to control periods than less compatible dyads. Less compatible individuals might choose the option to split from the former opponent to reduce the anxiety created by post-conflict interactions. Furthermore, reconciliation may be unlikely to occur among less compatible partners, since the benefit gained from such relationships is likely small, whereas fission represents a less problematic option to cope with post-conflict uncertainty, particularly given the lack of evidence for valuable relationships between the spider monkeys. The effect of components of relationships on the latencies of friendly and aggressive behaviour after a fusion also contributed to identifying the function of friendly and aggressive behaviour in such critical contexts. Individuals with riskier relationship engaged sooner in friendly and aggressive behaviours at fusion events. Dyads sharing a more risky relationship may experience more uncertainty over their relationship than less risky dyads, which, based on the behavioural variables that loaded onto risk, are more likely to exchange

aggressive interactions. That uncertainty therefore, may provide the motivation to signal the communication of good intentions to reduce likelihood of aggression. Dyads characterised by high compatibility, in contrast, experienced longer latencies to aggression compared to less compatible dyads.

7.2 Limitations and future directions

The results obtained with the PCA yielded only two components of relationship and neither component could be characterised as Value. Several reasons might explain the failure to find Value as one component of relationship quality in my study, which was predicted to be present based on Cords and Aureli (2002). First, one of the variables that define valuable relationship is agonistic support. This variable was taken into account in my data collection, but was witnessed only a few times during the course of my study. Spider monkeys do engage in coalitionary aggression within and between communities as well as territorial incursions. This is particularly evident among males (van Roosemalen & Klein, 1988; Campbell, 2006; Wallace, 2008) and has been witnessed in my own study communities (Valero et al., 2006; Aureli et al., 2006), therefore the lack of such observations during my study points to the importance for long-term uninterrupted studies of social dynamics. Clearly, spider monkeys do have valuable relationships; I just failed to garner sufficient evidence to demonstrate it during my period of data collection. A further reason for the lack of relevant data may be attributed to the advent of two hurricanes that altered the normal distribution of the spider monkeys' behaviour for 11.5 of the 18 months of my study duration. As a consequence, it is possible that behavioural mechanisms were altered in such a way that behavioural variables relevant for assessing Value were not possible to record. Furthermore, dyadic relationships are dynamic and subject to fluctuate over time (Aureli & Schaffner, 2008). For example, the finding of male-male intragroup coalitionary aggression at two different field sites (Valero et al. 2006; Campbell, 2006) might indicate that despite males' philopatry and presumed high quality bonds (Fedigan & Baxter, 1984; Ahumada, 1992), dramatic changes in the quality of their relationships might occur. Further studies and more long-term studies are warranted on several fronts. In spider monkeys it is important to further understand the components of social relationships and role that Value plays in their relationships. There is also a wider need for more studies that take an

objective approach to understanding animal social relationships. My study represents only the third of its kind to evaluate social relationships using such an approach (Fraser, et al., 2008; Fraser & Bugnyar, 2010).

The absence of reconciliation and other post-conflict behavioural management mechanisms, among the spider monkeys I studied, might be explained by a few factors. It is possible that aggressive conflicts did not disturb the relationships of the individuals in the majority of conflicts recorded, which is particularly likely if they occurred within dyads that had low compatibility and potentially low value. This view is further supported as individuals sharing compatible relationships were rarely involved in aggressive interactions. Nevertheless, further post-conflict interactions might be revealed by a larger dataset with a greater number of PC-MC pairs. Spider monkeys did not engage in aggressive interactions frequently. Furthermore, the occurrence of two hurricanes during the data collection impacted enormously on spider monkeys' social interactions to the point that I had to use data on aggressive interactions collected by a previous field worker on the same groups of spider monkeys. Therefore, it may be a case of continuing to build upon this existing dataset using periods of time that are not affected by the impact of hurricanes. Furthermore, additional studies of post-conflict behaviour are warranted at different field sites and for different species of spider monkey. Numerous studies have been carried out on chimpanzees and several species of macaque monkeys and the full picture of post-conflict behaviour may only now be emerging (Fraser & Aureli, 2008; Fraser, et al., 2009). In addition, studies on captive groups are also needed as it is possible to detect greater detail in behaviour in these settings.

Fission was the only post-conflict behaviour performed by the two communities of spider monkeys. This demonstrates that splitting from the opponents' subgroup is a means to cope with post-conflict uncertainty and species living in societies characterised by high FF dynamics might benefit from that option. Further research is warranted to examine the role fission has in managing conflict in other species. Such comparative approaches might shed light on the convergent evolutionary processes regulating conflict management in species living in social organisations characterised by high FF dynamics.

Although my study provides information regarding the effects of hurricane disturbance in the short term, more studies are warranted to understand how the effect of such disturbances impact upon animal populations on the long term. In fact, it has been suggested that sites impacted by hurricanes should be followed up for at least a decade to draw conclusion on the damage and mortality caused to the forest structure, which in turn affects animal populations (Everham & Brokaw 1996). My data on the behavioural dynamics and dietary adjustments displayed by the spider monkeys have important implications for conservation and additional, more long-term information about the recovery of the spider monkeys and their habitat would provide further information relevant for conservation in a part of the world that is ear-marked for strong impacts from climate change (Orellana, Espadas, Conde & Gay, 2009).

Despite the rather quick adaptation of the two communities of spider monkeys to the hurricanes, it is unknown what consequences such behavioural adaptation would have on social dynamics over the long term. Furthermore, the change in forest structure caused by the strong winds might have indirect medium to long term consequences on the distribution, community size and ranging patterns of the non-human primates living in reserve. Moreover, the capacity to recover from such disturbances is likely affected by the extension of the forest that a given animal population inhabit. Animals living in fragmented forests will not be able to increase their range indefinitely in search of dispersed feeding resources. Although my study did not provide information on the extension of the forest area used after the hurricane, it is likely that reduced subgroup size and the relative separation of small subgroups from one another had led to at least some individuals using areas of the forest that were previously not visited by any members of their respective communities in order to provide every single subgroup with sufficient amount of nutrients while, at the same time, avoiding fusion and increased subgroup size. Thus, further studies are warranted to examine the influence of natural disturbances on animal populations confined to fragmented forest patches which are already affected by a reduced habitat (Rangel-Negrín, Alfaro, Valdez, Romano & Serio-Silva, 2009). Moreover, hurricanes are expected to increase in intensity as a result of global warming, a tendency that has been confirmed during the past three decades (Webster, Holland, Curry & Chang, 2005; Trenberth, 2005; Hoyos et al., 2006) and given that

2010 it is currently an "el niño year" it is likely that further natural disturbances are forthcoming on the Yucantan Peninsula. More research on spider monkeys' adaptability to such disturbances is of primary importance for conservation purposes especially given the eligibility of such primates as bioindicators due to their long lifespan and interbirth intervals.

7.3 Conclusions

My study provided an original contribution to the understanding of the mechanisms that regulate conflict management in spider monkeys. Spider monkeys' quality of relationship is a key aspect in determining the modality of conflict prevention and resolution. Male-male relationships were characterised by high risk potential compared to other sex combination. I provided evidence that this aspect of male-male relationships is regulated by the use of good intention signals in contexts of high tension. Instead, in the aftermath of a conflict, potential risk is reduced by avoidance of former opponent achieved by fission. This study provided evidence that high FF dynamics play an active role as post-conflict mechanisms. Fission is a viable option in circumstances where reconciliation does not benefit the individuals that engaged in aggressive conflicts or when high risk is entailed in reconciliation or when simply sharing the former aggressors subgroup is untenable. Furthermore, high FF dynamics represent the strongest filter in the prevention of aggression by avoiding circumstances that can likely give rise to conflicts of interest. This goal is achieved by adjusting subgroups size when feeding resources are scarce and contest competition is likely to occur. A clear demonstration of such mechanisms is provided by the effect two almost consecutive hurricanes had on FF dynamics of the two communities of spider monkeys studied. This natural experiment did also evidence the high behavioural flexibility of spider monkeys' ecology by revealing the adaptability of this species to a disturbed environment.

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Appendix A

Subgrouping index, Eastern community

	be	ce	ch	cl	fl	he	hm	jo	kl	li	lo	mr	pa	tl	tn	
be																
ce		0.07														
ch		0.07	0.33													
cl		0.08	0.43	0.28												
fl		0.08	0.38	0.39	0.41											
he		0.07	0.37	0.17	0.33	0.26										
hm		0.18	0.89	0.26	0.26	0.32	0.37									
jo		0.05	0.17	0.25	0.28	0.18	0.26	0.21								
kl		0.07	0.31	0.20	0.34	0.32	0.45	0.27	0.31							
li		0.14	0.21	0.14	0.32	0.20	0.33	0.21	0.12	0.24						
lo		0.07	0.32	0.98	0.25	0.38	0.17	0.17	0.26	0.23	0.15					
mr		0.07	0.29	0.32	0.28	0.96	0.26	0.10	0.21	0.33	0.18	0.27				
pa		0.77	0.04	0.06	0.07	0.06	0.06	0.06	0.01	0.07	0.12	0.07	0.07			
tl		0.05	0.41	0.24	0.93	0.43	0.42	0.20	0.32	0.42	0.36	0.18	0.24	0.06		
tn		0.14	0.31	0.29	0.43	0.41	0.28	0.19	0.34	0.29	0.27	0.19	0.26	0.05	0.44	
ve		0.09	0.39	0.37	0.50	0.44	0.24	0.35	0.33	0.31	0.21	0.33	0.38	0.04	0.44	0.89

Appendix B

Proximity score, Eastern community

	be	ce	ch	cl	fl	he	hm	jo	kl	li	lo	mr	pa	tl	tn	ve
be																
ce		0.00														
ch		0.00	0.03													
cl		0.00	0.05	0.00												
fl		0.00	0.02	0.03	0.02											
he		0.04	0.00	0.00	0.00	0.00										
hm		0.06	0.12	0.01	0.03	0.01	0.02									
jo		0.00	0.00	0.00	0.00	0.03	0.02	0.00								
kl		0.00	0.02	0.00	0.00	0.01	0.05	0.01	0.00							
li		0.01	0.01	0.00	0.00	0.01	0.09	0.13	0.00	0.00						
lo		0.01	0.00	0.11	0.00	0.03	0.02	0.03	0.06	0.00	0.00					
mr		0.05	0.00	0.04	0.00	0.07	0.03	0.00	0.00	0.01	0.01	0.05				
pa		0.11	0.06	0.00	0.00	0.00	0.01	0.10	0.00	0.00	0.00	0.06	0.00			
tl		0.00	0.00	0.00	0.06	0.04	0.02	0.10	0.00	0.01	0.05	0.00	0.00	0.00		
tn		0.17	0.00	0.00	0.00	0.02	0.03	0.01	0.00	0.04	0.04	0.00	0.00	0.00	0.14	
ve		0.00	0.00	0.01	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.10

Appendix C

Grooming score, Eastern Community

	be	ce	ch	cl	fl	he	hm	jo	kl	li	lo	mr	pa	tl	tn	ve
be																
ce		0.00														
ch		0.00	0.00													
cl		0.00	0.00	0.00												
fl		0.00	0.00	0.00	0.00											
he		0.01	0.00	0.00	0.00	0.00										
hm		0.00	0.01	0.00	0.01	0.00	0.00									
jo		0.00	0.00	0.00	0.00	0.00	0.01	0.00								
kl		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00							
li		0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00						
lo		0.01	0.00	0.01	0.00	0.00	0.01	0.01	0.01	0.00	0.00					
mr		0.02	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00				
pa		0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
tl		0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
tn		0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
ve		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03

Appendix D

Grooming symmetry, Eastern community

	be	ce	ch	cl	fl	he	hm	jo	kl	li	lo	mr	pa	tl	tn	ve
be																
ce	-															
ch	-	-														
cl	-	0.00	-													
fl	-	-	-	-												
he	0.33	-	-	-	-											
hm	-	0.17	-	0.00	-	-										
jo	-	-	-	-	-	0.00	-									
kl	-	-	-	-	-	-	-	-								
li	-	0.00	-	-	0.00	0.00	0.00	-	-							
lo	0.00	-	0.28	-	-	0.00	0.00	0.30	-	-						
mr	0.00	-	-	-	0.11	-	-	-	-	0.00	-					
pa	0.27	-	-	-	-	-	-	-	-	-	0.00	-				
tl	-	-	-	0.40	-	-	-	-	-	-	-	-	-			
tn	0.00	-	0.00	-	-	0.00	-	-	-	-	-	-	-	-		
ve	-	-	0.00	0.00	-	-	-	-	-	-	-	-	-	-	0.46	

Appendix E

Agonistic support, Eastern community

	be	ce	ch	cl	fl	he	hm	jo	kl	li	lo	mr	pa	tl	tn	ve
be																
ce	-															
ch	-	0.25														
cl	-	-	-													
fl	-	-	-	-												
he	-	-	-	-	-											
hm	-	-	-	-		0.25	-									
jo	-	-	-	-	-	-	-									
kl	-	-	-	-	-	-	-	-								
li	-	-	-	-	-	-	-	-	-							
lo	-	-	-	-	-	-	-	-	-	-						
mr	-	-	-	-	-	-	-	-	-	-	-					
pa		0.5	-	-	-	-	-	-	-	-	-	-				
tl	-	0.3333333	-		0.2	0.3333333	-	-	-	-	-	-	-			
tn	-	-	-		0.1	0.1111111	-	-	-	-	0.5	-	-	-		
ve	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0909091	

Appendix F

Aggression rate, Eastern community

	be	ce	ch	cl	fl	he	hm	jo	kl	li	lo	mr	pa	tl	tn	ve
be	0															
ce	0	0														
ch	0.0007097	0.0001239	0													
cl	0	0	0	0												
fl	0.0007424	0	0	0	0											
he	0	0.0002727	0	0	0	0										
hm	0	0	0	0	0	0	0									
jo	0	0	0.0002495	0.0003547	0	0	0	0								
kl	0	0	0.0002218	0.0005042	0.0002205	0	0.0002606	0	0							
li	0.0013727	0	0.0003439	0	0	0	0	0	0	0						
lo	0.0007097	0	5.655E-05	0.0001199	0	0	0.0001122	0.0002464	0	0	0					
mr	0	0	0	0	7.882E-05	0	0	0	0.0002192	0	0.0001038	0				
pa	0	0	0.0006854	0	0	0	0.000994	0	0	0.0013559	0	0	0			
tl	0	0.0001482	0	0	0.0001296	0	0	0	0	0.0003676	0	0.0001301	0	0		
tn	0	0	0.0003053	0	0.0001147	0.000547	0	0.0002599	0	0	0	0.0002313	0.0011955	0.0001218	0	
ve	0	0	0.0001043	0	0	0	0	0	0.0002531	0.0003621	0.0001036	0	0	0	0	0

Appendix G

Successful grooming solicitation, Eastern community

	be	ce	ch	cl	fl	he	hm	jo	kl	li	lo	mr	pa	tl	tn	ve
be																
ce	-															
ch	-	-														
cl	-	-	-													
fl	-	-	-	-												
he	-	-	-	-	-											
hm	0.00	1.00	-	0.50	-	-										
jo	-	-	-	-	-	-	-									
kl	-	-	-	-	-	-	-	-								
li	-	-	-	-	1.00	0.86	-	-	-							
lo	-	-	0.65	-	-	0.50	0.33	0.50	-	-						
mr	1.00	-	-	-	0.71	-	-	-	-	1.00	-					
pa	0.57	-	-	-	-	-	-	-	-	-	0.33	-				
tl	-	-	-	1.00	-	-	-	-	-	-	-	-	-			
tn	0.00	-	-	0.00	-	0.50	-	-	-	-	-	-	-	-		
ve	0.00	-	1.00	1.00	-	-	-	-	-	-	-	-	-	-	0.74	

Appendix H

Embrace rate, Eastern community

	be	ce	ch	cl	fl	he	hm	jo	kl	li	lo	mr	pa	tl	tn	ve
be																
ce		0.000														
ch		0.000	0.001													
cl		0.000	0.002	0.000												
fl		0.000	0.000	0.000	0.000											
he		0.000	0.000	0.000	0.000	0.000										
hm		0.005	0.000	0.000	0.000	0.002	0.000									
jo		0.000	0.000	0.000	0.000	0.000	0.000	0.000								
kl		0.000	0.003	0.000	0.000	0.002	0.003	0.000	0.000							
li		0.013	0.010	0.000	0.004	0.000	0.000	0.017	0.000	0.000						
lo		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000					
mr		0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.003	0.000	0.000				
pa		0.003	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.017	0.000	0.000			
tl		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
tn		0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
ve		0.000	0.003	0.001	0.001	0.001	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Appendix I

Subgrouping index, Western community

	av	ba	bc	bt	cc	cd	co	cq	cr	cu	en	ev	fc	fe	fi	gb	ge	gr	is	ju	ky	lh	lr	ls	lu	mb	md	mo	ni	oc	of	pn	pq	ri	se	sf	so	tr
av																																						
ba	0.00																																				
bc	0.00	0.12																																			
bt	0.00	0.00	0.04																																		
cc	0.18	0.12	0.11	0.07																																	
cd	0.40	0.00	0.12	0.10	0.65																																
co	0.00	0.00	0.00	0.00	0.10	0.01																															
cq	-	-	-	-	-	-	-																														
cr	0.00	0.00	0.00	0.04	0.00	0.00	0.00																														
cu	-	-	-	-	-	-	-	-																													
en	0.04	0.00	0.49	0.13	0.30	0.27	0.00	-	0.00																												
ev	0.32	0.13	0.08	0.02	0.00	0.11	0.00	-	0.00	-	0.00																										
fc	-	-	-	-	-	-	-	-	-	-	-	-																									
fe	0.18	0.00	0.00	0.00	0.18	0.18	0.00	-	0.00	-	0.00	0.07																									
fi	0.48	0.00	0.04	0.14	0.31	0.74	0.04	-	0.00	-	0.08	0.16	-	0.11																							
gb	0.28	0.21	0.11	0.00	0.00	0.10	0.00	-	0.00	-	0.00	0.82	-	0.00	0.18																						
ge	0.00	0.91	0.00	0.00	0.18	0.04	0.00	-	0.15	-	0.10	0.03	-	0.05	0.00	0.00																					
gr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-																			
is	0.40	0.06	0.00	0.12	0.06	0.00	0.00	-	0.08	-	0.00	0.00	-	0.07	0.00	0.00	0.00	-																			
ju	0.07	0.16	0.00	0.00	0.00	0.15	0.08	-	0.00	-	0.00	0.11	-	0.00	0.04	0.24	0.06	-	0.09																	
ky	0.00	0.00	0.00	1.05	0.00	0.03	0.00	-	0.00	-	0.12	0.00	-	0.00	0.12	0.00	0.00	-	0.18	0.00																
lh	0.24	0.00	0.06	0.10	0.17	0.19	0.00	-	0.00	-	0.05	0.13	-	1.00	0.16	0.13	0.05	-	0.10	0.04	0.09															
lr	0.10	0.16	0.00	0.00	0.00	0.04	0.00	-	0.00	-	0.00	0.03	-	0.07	0.09	0.08	0.00	-	0.21	0.09	0.00	0.05														
ls	0.00	0.00	0.00	0.00	0.00	0.00	0.20	-	0.00	-	0.00	0.00	-	0.00	0.00	0.00	0.00	-	0.04	0.00	0.00	0.00	0.00													
lu	0.29	0.08	0.04	0.01	0.01	0.11	0.04	-	0.00	-	0.02	0.94	-	0.08	0.12	1.00	0.00	-	0.02	0.08	0.01	0.14	0.07	0.01												
mb	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	0.00	-	0.00	0.03	-	0.08	0.00	0.08	0.07	-	0.00	0.05	0.00	0.06	0.00	0.10	0.04											
md	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
mo	0.21	0.04	0.00	0.00	0.29	0.21	0.00	-	0.03	-	0.07	0.15	-	0.07	0.23	0.22	0.00	-	0.09	0.04	0.00	0.13	0.45	0.00	0.18	0.00										
ni	0.00	0.00	0.00	0.00	0.00	0.08	0.00	-	0.00	-	0.00	0.04	-	0.00	0.00	0.12	0.00	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	0.00								
oc	0.00	0.00	0.00	0.31	0.00	0.00	0.00	-	0.00	-	0.00	0.00	-	0.00	0.03	0.00	0.00	-	0.12	0.00	0.25	0.00	0.05	0.00	0.02	0.06	-	0.04	0.00							
of	0.00	0.00	0.08	0.00	0.14	0.02	0.84	-	0.00	-	0.00	0.03	-	0.00	0.03	0.06	0.00	-	0.00	0.11	0.00	0.00	0.00	0.09	0.06	0.00	-	0.02	0.00	0.00						
pn	0.00	0.00	0.00	0.00	0.00	0.04	0.00	-	0.00	-	0.00	0.00	-	0.00	0.04	0.00	0.00	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	0.00	0.00	0.00	0.00					
pq	0.00	0.00	0.00	0.27	0.00	0.00	0.00	-	0.00	-	0.00	0.00	-	0.00	0.04	0.00	0.00	-	0.12	0.00	0.11	0.00	0.01	0.00	0.02	0.00	-	0.02	0.00	0.94	0.00	0.00				
ri	0.00	0.17	0.00	0.03	0.03	0.02	0.14	-	1.00	-	0.05	0.00	-	0.00	0.00	0.00	0.29	-	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	0.04	0.00	0.00	0.08	0.00	0.00			
se	0.00	0.00	0.00	0.00	0.00	0.00	0.20	-	0.00	-	0.00	0.00	-	0.00	0.00	0.00	0.00	-	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.10	-	0.00	0.00	0.00	0.10	0.00	0.00	0.00		
sf	0.00	0.00	0.00	0.00	0.06	0.00	0.00	-	0.00	-	0.00	0.00	-	0.00	0.00	0.00	0.10	-	0.17	0.06	0.00	0.03	0.00	0.00	0.04	0.89	-	0.00	0.00	0.06	0.09	0.00	0.00	0.00	0.00	
so	0.04	0.24	0.00	0.00	0.00	0.16	0.21	-	0.00	-	0.00	0.03	-	0.00	0.05	0.09	0.00	-	0.00	1.24	0.00	0.01	0.00	0.00	0.02	0.00	-	0.02	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00
tr	0.13	0.00	0.00	0.04	0.00	0.15	0.14	-	0.00	-	0.11	0.07	-	0.00	0.12	0.09	0.00	-	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	-	0.04	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.15

Appendix J

Proximity score, Western community

	av	ba	bc	bt	cc	cd	co	cq	cr	cu	en	ev	fc	fe	fi	gb	ge	gr	is	ju	ky	lh	lr	ls	lu	mb	md	mo	ni	oc	of	pn	pq	ri	se	sf	so	tr
av																																						
ba	-																																					
bc	-	0.00																																				
bt	-	-	0.00																																			
cc	0.03	0.07	0.00	0.00																																		
cd	0.01	0.00	0.00	0.00	0.12																																	
co	-	-	0.00	-	0.00	0.00																																
cq	-	-	-	-	-	-																																
cr	-	0.00	-	0.00	-	-	-																															
cu	-	-	-	-	-	-	-	-	-																													
en	0.00	0.00	0.09	0.00	0.01	0.21	-	-	-	-																												
ev	0.08	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00																											
fc	-	-	-	-	-	-	-	-	-	-	-	-																										
fe	0.00	-	-	-	0.01	0.00		-	-	-	-	0.00	-																									
fi	0.04	-	0.00	0.00	0.01	0.21	0.06	-	-	-	0.00	0.00	-	0.00																								
gb	0.00	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00	0.14	-	0.00	0.10																							
ge	-	0.03			0.07	0.00	-	-	0.00	-	0.00	0.00	-	0.00	-	-																							
gr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00																					
is	0.00	0.00	0.00	0.00	0.05	-	-	-	0.00	-	0.00	0.00	-	0.00	0.00	0.00	0.00	-																				
ju	0.00	0.00	-	-	-	0.01	0.00	0.00	-	-	0.00	0.00	-	-	0.00	0.00	0.00	-	0.00																			
ky	-	-	0.00	0.18	-	0.00	-	-	-	-	0.00	-	-	-	0.00	-	-	-	0.00	-																		
lh	0.00		0.00	0.00	0.00	0.11	0.00	-	-	-	0.00	0.00	-	0.23	0.00	0.16	0.00	-	0.04	0.00	0.00																	
lr	0.08	0.00	-	-	0.29	-	-	-	-	-	0.00	0.00	-	0.00	0.00	0.00	-	-	0.00	0.00	-	0.00															
ls	-	-	-	-	-	-	0.00	-	-	-	-	-	-	-	-	0.00	-	-	-	-	-	-	-															
lu	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	0.00	0.12	-	0.00	0.00	0.22	0.00	-	0.00	0.00	0.00	0.09	0.00	0.08													
mb	-	-	-	-	-	-	-	-	-	-	-	0.00	-	0.00	-	0.00	0.00	-	-	0.00	-	0.02	-	-	0.00												
md	0.50	-	-	-	1.00	3.75	-	-	-	-	0.00	-	-	0.00	0.00	-	-	-	-		-	0.00	0.00	0.00	-	-											
mo	0.37	0.00	-	-	0.12	0.00	-	-	0.00	-	0.00	0.03	-	0.00	0.00	0.00	0.00	-	0.00	0.07	-	0.00	0.05	0.00	0.01	0.00	0.07										
ni	-	-	-	-	-	0.00	-	-	-	-	-	0.00	-	-	0.00	0.00	-	-	-	-	-	-	-	-	0.00	-	-	-									
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so	0.00	0.00	-	-	-	0.00	0.00	-	-	-	-	0.00	-	-	0.00	0.00	-	-	0.00	0.01	-	0.00	-	-	0.00	-	-	0.00	-	-	0.00	-	-	-	-	0.00	
tr	0.00	-	-	0.00	0.00	0.00	0.00	-	-	-	0.34	0.06	-	-	0.05	0.09	-	-	0.00	-	-	-	-	-	0.04	-	-	0.00	-	-	0.00	-	-	-	-	-	-

Appendix K

Grooming score, Western community

	av	ba	cc	bt	cc	cd	co	cq	cr	cu	en	ev	fc	fe	fi	gb	ge	gr	is	ju	ky	lh	lr	ls	lu	mb	md	mo	ni	oc	of	pn	pq	ri	se	sf	so	tr
av																																					
ba	-																																				
cc	-		0.00																																		
bt	-	-		0.00																																	
cc		0.00	0.04	0.00	0.00																																
cd		0.00	0.00	0.00	0.00	0.00																															
co	-	-		0.00	-	0.00	0.00																															
cq	-	-	-	-	-	-	-	-																													
cr	-		0.00	-	0.00	-	-	-	-																												
cu	-	-	-	-	-	-	-	-	-	-																											
en		0.00	0.00	0.00	0.00	0.00	0.03	-	-	-	-																										
ev		0.02	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00																									
fc	-	-	-	-	-	-	-	-	-	-	-	-	-																								
fe		0.00	-	-	-	0.00	0.00	-	-	-	-	-	0.00	-																							
fi		0.00	-	0.00	0.00	0.00	0.02	0.00	-	-	-	0.00	0.00		0.00																						
gb		0.00	0.00	0.00	-	0.00	0.00	-	-	-	-	0.00	0.06	-	0.00	0.02																					
ge	-		0.03	-	-	0.04	0.00	-	-	0.00	-	0.00	0.00	-	0.00	-	-																				
gr	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-		0.00																			
is		0.00	0.00	0.00	0.00	0.00	-	-	-	0.00	-	0.00	0.00	-	0.00	0.00	0.00	0.00	-																		
ju		0.00	0.00	-	-	-		0.00	0.00	0.00	-	-	0.00	0.00	-	-	0.00	0.00	0.00	-		0.00															
ky	-	-		0.00	0.00	-		0.00	-	-	-	-	0.00	-	-	-	0.00	-	-	-		0.00	-														
lh		0.00	-		0.00	0.00	0.00	0.00	0.00	-	-	-	0.00	0.00	-	0.06	0.00	0.00	0.00	-		0.07	0.00	0.00													
lr		0.01	0.00	-	-	-	0.00	-	-	-	-	-	0.00	0.00	-	0.00	0.00	0.00	0.00	-	-		0.00	0.00	-		0.00										
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lu		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	0.00	0.02	-	0.00	0.00	0.01	0.00	-		0.00	0.00	0.00	0.00	0.00	0.00									
mb	-	-	-	-	-	-	-	-	-	-	-	-		0.00	-	0.00	-	0.00	0.00	-	-		0.00	-		0.00	-		0.00	0.00						
md		0.00	-	-	-	0.43	0.00	-	-	-	-	0.00	-	-	0.00	0.00	-	-	-	-	-	-	-		0.00	0.00	-	-	-							
mo		0.01	0.00	-	-	0.00	0.00	-	-	0.00	-	0.00	0.00	-	0.00	0.00	0.00	0.00	-		0.00	0.00	-		0.00	0.07	-		0.00	0.00	1.19						
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Appendix L

Grooming symmetry, Western community

	av	ba	cc	bt	cc	cd	co	cq	cr	cu	en	ev	fc	fe	fi	gb	ge	gr	is	ju	ky	lh	lr	ls	lu	mb	md	mo	ni	oc	of	pn	pq	ri	se	sf	so	tr
av																																					
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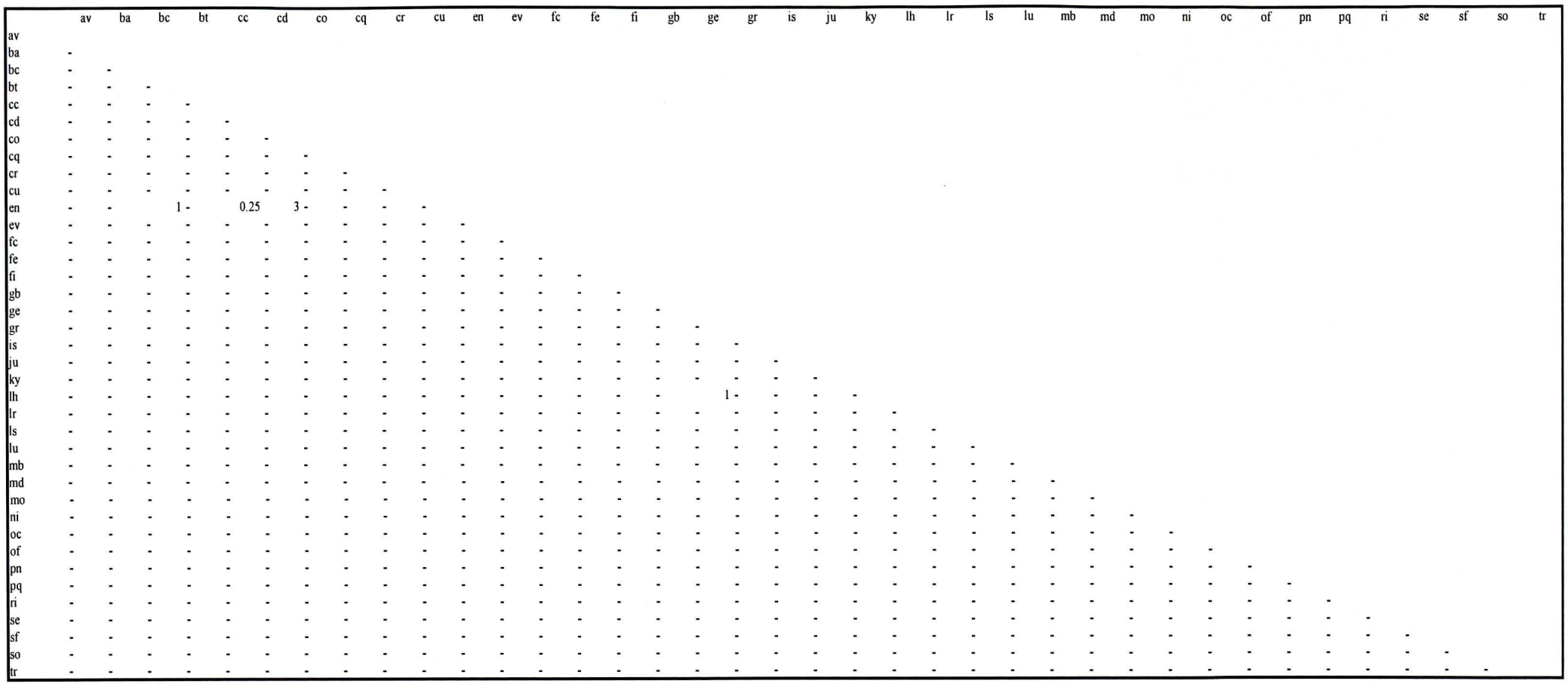
Appendix M

Agonistic support, Western community



Appendix N

Successful grooming solicitation, Western community

	av	ba	cc	bt	cc	cd	co	cq	cr	cu	en	ev	fc	fe	fi	gb	ge	gr	is	ju	ky	lh	lr	ls	lu	mb	md	mo	ni	oc	of	pn	pq	ri	se	sf	so	tr
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Appendix O

Aggression rate, Western community

	av	ba	bc	bt	cc	cd	co	cq	cr	cu	en	ev	fc	fe	fi	gb	ge	gr	is	ju	ky	lh	lr	ls	lu	mb	md	mo	ni	oc	of	pn	pq	ri	se	sf	so	tr
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Appendix P

Embrace rate, Western community

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